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INTRODUCTION

The four papers in this issue of the Journal were among those presented at a symposium sponsored by the International Society for Comparative Psychology at the XXIVth International Congress of Psychology at Sydney, Australia in 1988. These papers illustrate the recent resurgence of interest in the study of laterality as an evolutionary and developmental phenomenon and document the value of comparative study to our understanding of the process of behavioral lateralization.

Jeanette P. Ward

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LATERALITY IN ANIMALS

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We now know that laterality in various forms is a characteristic of a wide range of species, and that it apparently developed very early in evolution. Yet, some hundred years had to elapse after the discovery that there was lateralization, or asymmetry, for control of speech in the human brain, before any earnest attempts were made to discover or recognise the presence of laterality in nonhuman species (see Robinson, Becker & Camp, 1983). The reason for this delay appears to have been the belief that lateralization of brain function was a characteristic unique to the human species, placing our species above all other species.

This belief had been preceded by a well-developed mythology surrounding the sinistral-dextral dichotomy of handedness in humans (Corballis, 1983, pp. 1-9), and the belief that dextrality was also a uniquely human characteristic. It has been argued that shared tool use by humans caused laterality of limb use and, in turn, specialization of the left hemisphere for language (Frost, 1980; Bradshaw & Nettleton, 1982).

Thus, the population bias in handedness in humans was seen to be intimately related to our superior ability to use tools, and the population bias in lateralization of function in the cerebral hemispheres was seen to be the basis of our superior ability for language. Not surprisingly, these unique attributes afforded to the human species were reluctantly relinquished by many psychologists, some (e.g. Levy, 1974, 1979) clinging to them well after lateralization of function in the nervous system had been clearly demonstrated in more than one nonhuman species, in particular for control of singing in song-birds (Nottebohm, 1971; see later).

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LATERALITY OF LIMB USE

When in the 1950s and 1960s psychologists first set about looking for laterality* in nonhuman species, their aim was to see if they could find evolutionary evidence for asymmetry in humans. It is therefore not surprising that they chose to look for evidence of handedness in primates. The overall conclusion drawn from a large number of studies was that nonhuman primates do not have handedness like that of humans (e.g. Warren, 1958; Brookshire & Warren, 1962; or summarised in Corballis, 1983, pp. 113-116; Walker, 1980, pp. 348-351 and Warren, 1980, pp. 535-554). Although individual primates were found to show a preference for using one hand, in contrast to the human species, there was no overall bias in handedness at the population level, and it was generally considered that the individual lateralities in hand use were artifacts of the methods used to test the animals (Warren, 1980).

This view that nonhuman species lacked a population bias in laterality of limb use was reinforced by Collins' (1975) report that mice tested in a task requiring them to reach into a tube to obtain a food reward showed paw preferences as individuals but, as reported for nonhuman primates, there was no population bias of "pawedness". Moreover, raising the mice in right- or left-biased worlds was found to influence the distribution of paw preferences in the expected direction, confirming that experience is a factor influencing preference for limb use.

A recent report by MacNeilage, Studdert-Kennedy and Lindblom (1987) has, however, taken issue with the earlier reports of lack of handedness in nonhuman primates and, on re-examination of the data, the authors have reached the conclusion that there is more than simply suggestive evidence indicating that a number of species of macaques have a left-hand preference (see Ward, 1989, for a summary of reports of left-hand bias in prosimians). For primates in general, the authors propose that there is a left-hand preference for visually guided reaching movements and a right-hand preference for manipulation of objects. The remnants of this division of labour between hands may still be evident in humans despite our right-handedness, as there is some evidence that dextrals performing a task re-

*It should be noted that the terms laterality and asymmetry are used interchangeably when referring to functional differences between the left and right sides, but asymmetry is the term used for structural differences between the sides. This article will keep to the use of the term laterality unless there is a clear left-right structural difference involved.

quiring fast reaching for a visual target are more accurate than when using the left-hand (Guiard, Diaz & Beaubaton, 1983).

It is not my aim to discuss the relative merits of this particular theory. The data for handedness in primates are still a matter of controversy (see the peer review section following MacNeilage et al., 1987). If the earlier researchers had been able to move further away from the human species and look for laterality of limb use in birds, their search would have been more fruitful, and just as shattering for the belief that laterality of limb use at the population level was unique to humans and possibly caused by shared tool use. In a number of species of parrots and cockatoos there is a population bias in "footedness", as strong as that of handedness in humans.

Friedman and Davis (1938) reported left-footedness for manipulating food objects in several species of African parrots. Even though the sample sizes in this study were very small, it is important to note that this report was overlooked by those researchers looking for laterality in nonhuman species and focussing on primates. Australian cockatoos and parrots also have footedness for manipulating food objects (Rogers, 1981; and see Table 1). A strong bias for left-footedness was found in eight of the nine species scored. The exception was *Platycercus elegans*, the crimson rosella, which showed right-footedness.

Footedness appears to occur only in those avian species which use their feet in feeding. Pigeons do not manipulate food objects with their feet, and Güntürkün, Kesch and Delius (1988) have recently reported the absence of footedness in pigeons tested by sticking a piece of tape on the tip of the beak and scoring the foot used in the first attempt to remove it (see Table 1). They found no bias in foot use at either the population or individual level. This lack of footedness in pigeons is species rather than task specific: they tested a small number of parrots on the same task and found the preferred foot used to remove the tape was consistent with their footedness for manipulation of food objects. Ducker, Luscher and Schulz (1986) have observed right-footedness (100%) in gold finches, *Carduelis carduelis*, tested on a task requiring the birds to open doors and catches using the beak and a foot in order to obtain a food reward. These data support the general hypothesis that limb use preferences occur only in species which use their limbs for manipulative activities (Walker, 1980).

We therefore decided to test this hypothesis using a species of parrot which does not manipulate objects with its feet. Budgerigars were tested for foot use in removal of a piece of sticky tape from the beak (Workman & Rogers, in preparation; see Table 1). Nine individuals were scored for a mean of 20 trials each. They showed no footedness either at the population level or as individuals. This supports the

TABLE 1
Footedness in Birds.

	Species	Percentage left-footedness	Number of observations
A	Galah (*Cacatua roseicapilla*)	89	68
	Sulphur crested cockatoo (*Cacatua galerita*)	87	113
	Little corella (*Cacatua sanguinea*)	93	15
	Long-billed corella (*Cacatua tenuirostis*)	89	19
	Pink cockatoo (*Cacatua leadbeateri*)	100	24
	Yellow-tailed black cockatoo (*Calptorhynchus funereus*)	100	7
	Gang-gang (*Callocephalon fimbriatum*)	100	38
	Crimson rosella (*Platycercus elegans*)	23	90
	Yellow rosella (*Platycercus f. flaveolus*)	100	6
B	Chicken (*Gallus gallus*)	32 (±3)	240 (6 animals)
C	Budgerigar (*Melopsittacus undulatus*)	* 53 (±9)	180 (9 animals)
	Chicken (*Gallus gallus*)	* 16	37 (37 animals)
	Pigeon (*Columbia livia*)	* 53	250 (50 animals)

Foot use in feeding or in attempting to remove a piece of sticky tape from the beak (the latter scores being marked by asterisks). For the first nine species listed under A, the percentage of left-footedness refers to the percentage of animals using the left foot to manipulate food objects, the animals being observed either in captivity or in their natural environment. All of these species show significant footedness (data quoted from Rogers, 1981). Additional data (not included here) of repeated observations of foot use by single individuals indicate that individuals have a consistent foot preference. The results listed under B are for the foot used to initiate a scratching bout during feeding. There were 40 such scores for a total of 6 animals, and the data are given as a mean and standard error (in brackets). Note the right-footed bias. The result for chickens listed under C is the percentage of animals using the left foot to remove a piece of sticky tape from the beak (one observation, of the first movement made, per bird). Again, note the right-footed bias. Also listed under C are mean scores, with standard errors, for repeated attempts of budgerigars or pigeons to remove a piece of sticky tape from the beak. There is no footedness in these species. The data for pigeons are quoted from Güntürkün, Kesch and Delius (1988). Means and standard errors (in brackets) are given where it was possible to make repeated measures on given individuals.

hypothesis that laterality in limb use occurs only when the feet are used to manipulate objects.

Yet, contrary to this hypothesis we have recently found footedness in a species which does not use its feet to manipulate objects. Chickens (*Gallus gallus*) do not use their feet to pick up and manipulate food or other objects, but they frequently scratch the ground when searching for food. Workman and Rogers (in preparation) scored the first foot used to rake the ground at the beginning of a bout of ground scratching. Six animals were scored for 40 scratching bouts each. Though both feet are used in this behaviour, there was a significant tendency to initiate a bout of ground scratching by using the right foot (68 ± .03% right-footedness, mean and standard error; $p < .05$). When 10-day old chicks were tested on the task requiring removal of sticky tape from the beak a stronger right-foot bias was found (84%; $p < .01$; the first foot chosen to scratch the tape was scored, thus giving one score per individual, n = 37). Apparently, it is not manipulative ability alone which confers footedness on avian species, but also active use of the feet in feeding or searching for food.

The fact that chickens show right footedness in searching for food is not insignificant as they have dominance of the right eye in tasks requiring them to search for food and to perform visual discrimination learning. By testing chickens monocularly on a task requiring search for food grains Andrew, Mench and Rainey (1982) and Zappia and Rogers (1987) have shown that the right eye learns to discriminate grains from small pebbles more rapidly than does the left eye. Also chickens trained binocularly on a visual discrimination task have dominance of the right eye for recall of the task (Gaston & Gaston, 1984). Given this dominance of the right eye in searching for food and the fact that chickens have laterally placed eyes with only a small area of binocular overlap, it makes logical sense that chickens have right footedness for initiating scratching of the ground to expose grains of food.

The pigeon has the same lateralization of eye use in visual discrimination learning as does the chicken (Güntürkün, 1985), but it does not have footedness and it does not use the feet to scratch the ground while feeding. This suggests that footedness (in both feeding and non-feeding tasks) in avian species may have developed secondarily to lateralization of visual functions at the perceptual level, and only in species which actively use their feet in feeding, either to manipulate the food or to uncover it by scratching the ground.

In other words, if the feet are used in feeding, laterality of foot use may occur as a *result* of the constraints placed upon it by lateralization in perceptual or cognitive processes linked to either eye.

If one tentatively considers extending this hypothesis to mammalian species, it may be argued that handedness followed on from

the presence of laterality at the cognitive or perceptual level of brain organisation, rather than it being an antecedent of the latter, as implied by McNeilage et al. (1987) and as stated by Kimura (1979) and Frost (1980) (see later for evidence of lateralization of cognition in mammalian species).

Unfortunately, we know nothing as yet of lateralization of function in the forebrain of parrots or cockatoos, except that *Amazona amazonica*, which is 75% left-footed (Friedman & Davis, 1938), does not have lateralization of control of vocalisation (Nottebohm, 1976b). Nevertheless, it is highly likely that parrots and cockatoos do have laterality for other forebrain functions. Zebra finches, for example, have no, or possibly only slight, laterality for control of their vocalisations (Nottebohm, personal communication) but they show strong functional laterality for copulation responses: the male views the female with his right eye when performing courtship behaviour (Workman & Andrew, 1986). The right footedness of *Platycerus elegans* may indicate a different, if not inverted, laterality at higher levels of central processing in this species.

With the development of greater manipulative ability (e.g. with the evolution of the opposable thumb in primates) laterality of limb use, though perhaps originally developed for feeding, would become manifest in a range of activities, including tool use. As primates became more able to adopt an upright posture they needed to use the originally non-specialised (right) fore-limb less often for supporting the body. MacNeilage et al. (1987) argue that this may have altered the evolutionary course of handedness, as the right hand could now take over and specialise for manipulation while the left remained specialised for visually guided reaching. In birds there is no possibility for simultaneous use of both limbs to "handle" an object as one limb is always needed to support the body. Thus, in birds the foot first specialised to hold food may be retained for all manipulative functions. So saying, one must recognise that the question as to why some species are left-footed and others right-footed remains open. It may perhaps depend on the particular direction of laterality in the perceptual processes used in feeding behaviour in the given species or, indeed, in the given individual. Alternatively, it may depend on the type of searching strategy which the particular species utilises in feeding. Andrew, Mench and Rainey (1982) have found that the left eye of the chicken is specialised for analysis of the spatial position of objects, whereas the right eye is specialised for discriminating and categorising objects, particularly food versus non-food, irrespective of their position in space. Left-footedness may occur in species in which foraging involves greater use of spatial cues rather than detailed discrimination of food objects from the background, and *vice versa* for right-footed species.

LATERALITY OF COGNITIVE FUNCTION

It is in perceptual and cognitive functioning that we find the clearest examples of laterality in animals at the population level. In Japanese macaques the left hemisphere is specialised for processing their species-specific vocalisations (Peterson, Beecher, Zoloth, Moody & Stebbins, 1979). Denenberg (1981) has shown that rats have lateralization of "affective behaviour", measured in terms of taste aversion and muricide. The data suggest that the right hemisphere is more fearful than the left, and that the left hemisphere can inhibit this aspect of functioning in the right (Denenberg & Yutzey, 1985). Denenberg's extensive studies on laterality in rats have led him to conclude that the right hemisphere of this species is specialised for "strong emotional" behaviours and some spatial processes (Denenberg, 1984b).

In a series of experiments testing rats in operant conditioning tasks Bianki (1983, 1988) has demonstrated that the left hemisphere is specialised for processing sequentially presented visual stimuli while the right is specialised for processing simultaneously presented visual stimuli. Bianki's findings are strikingly reminiscent of the lateralized organisation present in humans.

These lateralities of hemispheric functions in rats are correlated with asymmetries in the structure of the cortex and in the cellular densities. In male Long-Evans rats most areas of the cortex are thicker on the right side than the left (Diamond, 1984), and this greater thickness results from having a higher number of both neuronal and glial cells (McShane et al., 1988), although it is not known whether, or how, these structural differences pertain to functional lateralization.

It should be noted again that this population bias in cortical laterality in rats is not manifest in "pawedness" at the population level, although there is at least one motor output pattern which shows a population bias. Rats handled in early life show a left side bias in the direction in which they make their first move when placed in the open field (Sherman, Garbanati, Rosen, Yutzey & Denenberg, 1980). Intact, non-handled rats show no spatial bias, but ablation of the left hemisphere generates a left-side bias while ablation of the right generates a less marked right-side bias. Hence, Sherman et al. (1980) deduced that handling in early life produces a right hemispheric dominance, and so unmasks population laterality in the direction of moving off in the open field.

The direction of the first move made in the open field is not related to turning behaviour in rats, as studied by Glick (see Glick, 1983, and Glick & Shapira, 1985). Glick has looked at turning or circling behaviour which occurs in a preferred direction in the individ-

ual either spontaneously at night or after treatment with drugs such as amphetamine or apomorphine. Examination of a group of over 600 rats revealed that 54.8% circled to the right and this was calculated to be a significant population bias (Glick 1983, p. 18), although it is by no means an impressively sized bias. Ross, Glick and Meibach (1981) and Denenberg et al. (1982) have shown a similarly sized significant population bias in the direction in which neonatal rats hold their tails, the actual direction of the bias depending on both the sex and strain of the rats.

The direction of circling in an individual correlates with the relative concentrations of dopamine in the striata on the left and right sides of the brain: the rats rotate contralaterally to the side with the higher dopamine level. Moreover, tail posture in neonates predicts both the rotational bias and dopamine asymmetry (Rosen, Finklestein, Stoll, Yutzey & Denenberg, 1984). Pawedness can be generated at the individual level by conditioning, and there is some suggestion that in this case it correlates with laterality in dopamine levels (Schwarting, Nagel & Huston, 1987). Dopamine levels are higher in the amygdalae ipsilateral to the paw used in the task. It would be interesting to know how this relates to the direction of turning. That is, whether the direction of rotation is also changed by this conditioning process.

Thus, in rats there are individual lateralities at one level of brain organisation (in the striata and amygdalae) and a population bias at another level of organisation (cortex). Different types, degrees, and directions of asymmetry occur in different regions of the brain. There is, however, no obvious hierarchical organisation as to which form of laterality occurs at the various levels of complexity in processing because, like the cortex, the hypothalamus also displays laterality of functioning at the population level. Implantation of oestradiol into either the left or right side of the hypothalamus of neonatal female rats causes different effects on sexual behaviour in adulthood (Nordeen & Yahr, 1982). Implanting oestradiol into the ventromedial nucleus on the left side of the hypothalamus was found to suppress lordosis by a mean of approximately 35%, while implants in the right ventromedial nucleus had no effect on this behaviour. Implants of oestradiol into the preoptic area on the right side of the hypothalamus elevated mounting by a two-fold factor, while implanting the equivalent region on the left side had no effect.

The hypothalamus of the rat also has laterality for control of hormonal output from the pituitary (Bakalkin et al. 1984). In Wistar rats, the right side of the hypothalamus has a higher concentration of luteinizing hormone releasing factor; in an albino rat strain it is the other way around.

Many of the earlier concepts of lateralized brain function incorporated the idea that it was present only in the cortex and required a corpus callosum to interconnect the two hemispheres so that one hemisphere (the left in most cases) could suppress the other (see Gazzaniga, 1974; Denenberg, 1981). Gazzaniga and Le Doux (1978) postulated that evolution of the corpus callosum was essential for the appearance of laterality in the brain. They based their argument on empirical evidence that lateralization of language in humans does not develop until the fibres in the corpus callosum are fully myelinated (Gazzaniga, 1974). It is not difficult to see that their general hypothesis for the presence or absence of laterality is human-centred and based on the original premise that laterality is unique to humans and their capacity for language. Denenberg (1981) extrapolated this idea to include all mammalian brains and developed a model to explain his data for laterality in rats (see earlier), involving suppression of the right hemisphere by the left via the corpus callosum. Berrebi et al. (1988) have now found evidence that handling increases the size of the corpus callosum in male rats aged 110 days, which certainly supports a role for the corpus callosum in functional laterality at the level of the cortex since, as discussed previously, handling unmasks laterality in the direction of moving off in the open field. Nevertheless, laterality in the hypothalamus cannot easily be tied to the corpus callosum unless the laterality in the hypothalamus is conferred upon it by higher centres in the cortex.

Evidence of laterality in the avian brain conclusively shows that the corpus callosum is not necessary for asymmetry to occur, as there is no corpus callosum in the avian brain. Pathways do cross from left to right in the avian brain in the supra-optic decussation and the tectal posterior and anterior commissures but these are small pathways. Also the supra-optic decussation does not connect homologous regions of the brain, the latter being the essential property of the corpus callosum and its chief attribute thought to be used by one side to inhibit the other and so generate functional lateralization.

The avian forebrain has some fine examples of laterality. In a number of species of song-birds, singing is controlled by the left hemisphere (in chaffinches, Nottebohm, 1971; in crowned sparrows, Nottebohm, 1976a; and in canaries, Nottebohm, 1977). Lesions of the hyperstriatum ventrale, pars caudalis (HVc) on the left side eliminate singing, whereas lesions of the right HVc have no effect. This striking finding has been widely quoted in terms of its analogy to the human condition with language on the left side, particularly given the parallels which have been drawn between the "syntactical" structure of bird song and human language. Yet, there is a distinct difference between the two systems. There are anatomical asymmetries associated

with the functional lateralization of language/speech in humans, but no structural asymmetries are present in the centres controlling singing in the song-birds.

In humans the region involved in speech comprehension (Wernicke's area) is larger on the left side (Geschwind and Levitsky, 1968), and damage to this area in adults leads to aphasia with the right side being unable to take over to produce speech. In contrast, birds have the full complement of structures which control singing on both sides of the brain. If the left HVc of canaries is lesioned in one reproductive season no singing will occur in that season, but in the next season the right HVc takes over and the full song repertoire is regained. It is not known how much, if any, of the previous season's song is retained. The function of the right HVc in an intact brain is not known. Perhaps it is used in analysis and comprehension of the songs of other birds, or in storing a memory of the individual's own song. Given the absence of a corpus callosum interconnecting homologous regions in the forebrain, one wonders how the left HVc suppresses the right HVc in the intact brain. Also why does the right HVc remain suppressed for the rest of the singing season when the left is lesioned? In other words, when the left HVc has been lesioned, why is there a delay until after the sex steroid hormone levels have subsided and re-elevated before the right HVc can take over and control singing? Elevated testosterone levels permit neurogenesis in the adult canary brain (Nottebohm, 1987, 1989), and this neural plasticity is clearly necessary for the right HVc to assume control of singing after lesioning the left. Possibly rising levels of testosterone at the beginning of the reproductive season are essential to trigger the combined processes of song production and neural plasticity. There are many interesting questions yet to be answered. It should be noted that in chaffinches, which unlike canaries do not embellish their song repertoire each season, the right HVc does not take over the control of song after the left HVc is lesioned (Nottebohm, 1987). Canaries are, according to Nottebohm, "open-ended learners" which retain neural and functional plasticity in adulthood, while chaffinches are "critical-period learners" which lose and never regain the ability to add to their repertoire.

As mentioned briefly before, the chicken (*Gallus gallus*) brain has laterality for a number of functions. Our original studies revealed laterality by injecting the protein synthesis inhibitor, cycloheximide (CXM) into either the left or right forebrain hemisphere in early life. Treatment of the left produced a permanent deficit in the ability to learn a task requiring the chick to discriminate between grains of food and small pebbles adhered to the floor (the 'pebble floor task') and retarded habituation to both visual and auditory stimuli (Rogers & Anson, 1979). Treatment of the right hemisphere did not affect

these behaviours. These results were subsequently confirmed by testing uninjected chicks monocularly. The avian nervous system has an anatomical feature which makes it admirably suited to studying laterality; viz. the optic nerves decussate completely so that the primary visual connections go only to the contralateral side of the brain (Cowan, Adamson & Powell, 1961). Thus monocular testing achieves the same unilateral input to the brain as does the complicated tachistoscopic presentation to humans of stimuli placed in the extreme peripheral fields of vision. In this respect, the bird brain may be considered as a "split-chiasma" mammalian brain.

When tested monocularly on the 'pebble floor' visual discrimination task, young male chicks using the right eye learn as well as binocularly tested controls, but in those tested using the left eye learning is retarded (Mench & Andrew, 1986; Zappia & Rogers, 1987). By the age of 23 days post-hatching this laterality in performing the pebble floor task has disappeared as both eyes now learn well (Rogers, 1990b).

The presence of this functional lateralization for visual discrimination learning in young male chicks correlates with a structural asymmetry in the visual projections from the thalamus to the visual Wulst, or hyperstriatum, of the forebrain (Boxer & Stanford, 1985; Rogers & Sink, 1988). The left side of the thalamus, which receives input from the right eye only, sends projections to hyperstriata on both sides of the forebrain. The right side of the thalamus, which receives input from the left eye only, projects to the right hyperstriatum but very few projections cross over to go the hyperstriatum on the left side. This better connectivity of the right eye to both sides of the hyperstriatum may well explain its superior performance in visual discrimination learning. By the beginning of the third week of life post-hatching the projections from the right side of the thalamus to the left hyperstriatum have developed and there is no longer any asymmetry in the organisation of these thalamofugal visual pathways. The loss of this structural asymmetry parallels the loss of functional laterality in visual learning ability on the pebble floor, suggesting a direct connection between the two.

Newly hatched female chicks have no asymmetry in the organisation of their visual projections from thalamus to hyperstriatum (Adret & Rogers, 1989) and no difference in visual learning ability between the left and right eyes (Zappia & Rogers, 1987). It is possible that the visual pathways develop over a different time-course in females and that they do have asymmetry in them at an age not yet sampled, possibly before hatching.

In young male chicks the left eye is more responsive to novel stimuli and shows more fear responses to a purple coloured bead (Andrew & Brennan, 1983). This form of laterality is also transient, dis-

appearing by the second week of life, which is earlier than the loss of asymmetry in the thalamofugal visual projections.

Young female chicks do not have laterality in their fear responses: both eyes of the female respond the same as the right eye of the male (Andrew & Brennan, 1984). Both eyes of the female and the right eye of the male have their full complement of contralateral visual projections from each side of the thalamus to the hyperstriatum, while the left eye of the young male is deficient in contralateral projections from thalamus to hyperstriatum (Adret & Rogers, 1989), which suggests at least some link between organisation of the visual pathways and fear responses to a bead.

Phillips and Youngren (1986) have found that unilateral injection of kainic acid into the right archistriatum of 5 day-old chicks reduces fear responses in the open field, whereas injection of the left archistriatum does not. It is, as yet, unclear how these results may link to lateralities in fear responses scored in monocular testing.

Interestingly, there is no sex difference in the effect of unilateral treatment of the forebrain with glutamate or cycloheximide. Treatment of either the left or right hemisphere reveals the same lateralization for visual discrimination learning in both males and females even though females tested monocularly on this task show no laterality (Rogers, 1986). The unilateral administration of drugs, therefore, reveals that females have laterality at deeper levels of brain processing (i.e. further removed from the level of perceptual input).

Chickens therefore exhibit laterality at several levels of neural organisation and there are sex differences at the perceptual level. The left and right eyes of male chickens perceive entirely different visual worlds, and there is asymmetry in the visual pathways which carry information from the mid-brain to the forebrain. Females have no asymmetry at the perceptual input level but, similar to males, they have functional asymmetry at higher levels of processing in the forebrain.

The left eye of the chicken is used for control of attack and copulation responses (Howard, Rogers & Boura, 1980; Bullock & Rogers, 1986; Rogers, Zappia & Bullock, 1985). For example, chicks treated with testosterone (or oestrogen) show elevated copulation scores when they are tested binocularly on standard hand-thrust tests, and also when they are tested with the right eye occluded (i.e. using the left eye only). In contrast, when they are tested with the left eye occluded (i.e. using the right eye only), they show no evidence of having been treated with the hormone; their scores for attack and copulation are not elevated above control levels.

Recently, we have shown that asymmetry for attack, at least, persists into adulthood. Adult hens with the left binocular area of the visual field occluded by “monocular polypeepers” have a low level of

agonistic behaviour, equivalent to that of hens wearing "binocular polypeepers". Those with occlusion of the right binocular field have a high level of agonistic behaviour, equivalent to that of controls not wearing polypeepers (Rogers & Workman, in preparation). Since this form of laterality is present in adults and in females, it is unlikely to depend directly on differential input to the forebrain caused by asymmetry in the visual projections. Alternatively, if asymmetry in the visual projections exists at some time during the early development of the female, this may confer a functional laterality on the forebrain which persists after the asymmetry in visual pathways has disappeared. For example, asymmetry in visual inputs to the hyperstriatum may establish an initial laterality in perceptual analysis and memory formation, which lays the foundations for subsequent differentiation of processing between the hemispheres.

DOMINANCE VERSUS DIFFERENTIAL USE OF THE HEMISPHERES

Laterality of brain function may involve complete dominance of one hemisphere over the other so that all of a given sort of analysis occurs on one side only, it may be a matter of relative degrees of involvement of the hemispheres in a given form of processing, or it may involve simultaneous but differential use of the hemispheres in performing a given function. The latter occurs in imprinting in the chicken.

The intermediate and medial parts of the hyperstriatum ventrale (IMHV) on the left and right sides of the forebrain are differentially involved in imprinting (Cipolla-Neto, Horn & McCabe, 1982; and see Horn, 1985, pp. 129-150). The memory of imprinting is stored in both the left IMHV and right IMHV for approximately the first 3 hours after training, but by some 15 hours later the right IMHV no longer retains its store of the memory while the left does. On the right side the memory store is shunted to some other region of the hemisphere. Horn and his colleagues demonstrated this by placing sequential lesions in the left and right IMHV regions after imprinting. In one group of chicks the right IMHV region was lesioned 3 hours after imprinting on day 1 of life (the memory of imprinting was retained by these animals), and then the left IMHV was lesioned some 23 hours later. After this sequence of lesions no memory of the imprinting was retained. In another group of chickens the left IMHV was lesioned 3 hours after imprinting (memory being unaffected by this), and then 23 hours later the right IMHV was lesioned. Subsequently, these chicks were found to have memory of the imprinting stimulus. Thus, the long-term memory of imprinting is consolidated in different regions of the left and right hemispheres. This differential use of the

hemispheres may possibly be the reason why imprinting forms a strong and stable memory trace (Rogers, 1986).

Both hemispheres are also used differentially when young chicks learn a passive avoidance task which involves pecking of a bead coated with the noxious tasting substance, methyl anthranylate. There is laterality in the time course of memory events occurring in each hemisphere. The right eye shows a brief period of improved recall 30 to 32 minutes after training, while the left does so at 25 minutes after training (Andrew & Brennan, 1985).

In the same task Rose & Csillag (1985) have shown laterality in neuronal metabolism using the radioactive 2-deoxyglucose technique. This is an example of 'metabolic' dominance. One can say 'dominance' since the chicks were tested using both eyes, the bead was held in the binocular field of vision and competition between the hemispheres could occur. It is possible to make inferences about laterality from tasks in which birds are tested monocularly, but dominance can be determined only by testing them binocularly. The latter requires competition and one side "winning" over the other.

Subcellular structural components in the IMHV, such as synaptic apposition length, also change asymmetrically after training on the passive avoidance bead task (see Stewart, Rose, King, Gabbott & Bourne, 1984), some of the changes being greater on the left side, others on the right.

Finally, it is worth mentioning that birds spend a considerable amount of their sleeping time with one hemisphere asleep while the other is awake. This is monocular sleep in which only the hemisphere contralateral to the closed eye shows a lateralized sleep pattern of electrical activity (Ball, Amlaner, Shaffery & Opp, 1988). The laterality in brain function generated thus is only transient, but it may be essential to behaviour and possibly memory formation. It is possible that a bird sleeping in its left hemisphere only would be more responsive to novel stimuli, and subsequently show a greater likelihood of attacking, compared to one sleeping in its right hemisphere only. We do not yet know whether one hemisphere sleeps more than the other, or whether performing certain sorts of behaviour may trigger more sleep on one side than the other.

LATERALIZATION IN INDIVIDUALS AND IN POPULATIONS

Up until now, there has been a tendency to underestimate the importance of laterality at the individual level, and to focus only on laterality in the population as a whole. This has resulted from an emphasis on looking for genetic/evolutionary explanations for laterality in humans, but, if a brain needs to be lateralized to function

efficiently, it may not matter on which side it conducts one set of functions versus the other, only that laterality is present in one direction or the other.

At least, this would be the case at the level of the individual. Nevertheless, if lateralization of brain function has a role in social behaviour, whether or not most (or even all) individuals in the social group are lateralized in the same direction may be influential. Indeed, in groups of young chickens the presence or absence of lateralization at the population level has been shown to alter the stability of the social hierarchy (Rogers & Workman, 1989). Chicks hatched from eggs exposed to light during incubation all have their brains lateralization in the same direction (see later); they have lateralization at both the individual and the population levels. Those hatched from eggs incubated in darkness have lateralization at the individual level, but not at the population level (Rogers, 1982; see later); half of the individuals have lateralization in one direction and half in the other. The social groups of chicks exposed to light during incubation form a more stable and rigid hierarchy, as measured in terms of their competition for access to a food source. The group structure of chicks hatched from eggs incubated in darkness was more variable from day to day, possibly because there was less predictability from individual to individual within the social group.

To summarise, for solitary behavioural performance the direction of lateralization for perception, cognition, footedness or handedness may not matter. However, the presence of a population bias in lateralization may well have some influence on social interaction and group structure. It is, of course, the latter situation which has concerned anthropologists with respect to handedness in the human population and shared tool use.

FACTORS AFFECTING THE DEVELOPMENT OF ASYMMETRY

In the chicken the direction of brain laterality is determined by differing amounts of light input received by the left and right eyes of the embryo (Rogers, 1982; Rogers 1986). During the last three or so days of incubation the chick embryo is oriented in the egg such that its left eye is occluded by its body and the right eye is exposed to receive light input entering the egg through the shell and membranes. The greater amount of light received by the right eye during the sensitive period just prior to hatching stimulates the growth of visual pathways from that eye in advance of those from the left eye.

If the embryo's head is withdrawn from the egg on day 19 or 20 of incubation, the right eye occluded and the left eye exposed to light, there is a reversal of both structural and functional laterality in the

brain. The asymmetry in the visual projections from thalamus to forebrain in male chicks is reversed (Rogers & Sink, 1988), and the functional lateralization for attack and copulation behaviour is reversed (Rogers, 1990a). Chicks hatched from eggs incubated in darkness show no population laterality for attack and copulation, but appear to retain laterality at the individual level (Zappia & Rogers, 1983). Thus, lateralized light input before hatching aligns the direction of laterality in the population, but it does not actually generate the asymmetry. (Only 2 hours of light is sufficient to do this; Rogers, 1982.) Compare the effects of handling in rats in which the early experience unmasks or generates a laterality not present in non-handled animals (Sherman et al., 1980; see earlier).

The hormone testosterone can also influence the development of laterality in male chicks (Zappia & Rogers, 1987). Treatment with testosterone on day 2 causes a reversal in the laterality of eye differences in performance on the visual discrimination, pebble floor task. Contrary to expectations, treatment of females with testosterone does not generate lateralized differences between the eyes; that is, it does not "masculinize" their brains.

Diamond (1985) has reported asymmetries in the thickness of various regions of the cortex of the rat. In males on the whole the right cerebral cortex is larger than the left, and the reverse is generally true in females. Ovariectomising females leads them to have the male-type pattern. Yet hormones are not the only variables determining thickness of the cortex as it is also affected by age and experience in enriched and impoverished environments. These latter factors also influence the degree of asymmetry between the left and right sides. Consistent with this, Berrebi et al. (1988) have shown effects of sex, early experience and age on various regions of the corpus callosum.

There are sex differences in the lateralized bias in tail posture adopted by neonatal rats, the exact nature depending on the strain (see Denenberg, 1984a), and Rosen, Berrebi, Yutzey & Denenberg (1983) have shown that this can be influenced by administering androgens prenatally. Females responded to treatment with testosterone showing a reversal in the bias of their tail posture but the treatment did not make them the same as males. There was no effect of testosterone treatment on the males.

Geschwind and Behan (1982) have postulated that testosterone may have a role in the development of laterality in the human brain and so account for at least some of the differences in behaviour between the sexes. Theirs is a rather unitary hypothesis giving testosterone a major, or even sole, role in determining laterality in the human brain. As the studies using the chicken brain as a model demonstrate, testosterone and environmental experience (light input) can both influence laterality, and these must both interact with genetic

factors (which are likely to determine the orientation of the embryo in the egg) to produce a final result in a given brain. No single factor can be separated out as the major or sole determinant in its own right.

Geschwind & Behan (1982) proposed that testosterone acts on the left hemisphere to retard its development, and thus high levels of testosterone in the foetus may cause an increased incidence of left-handedness and mental retardation, both occurring more frequently in males. High levels of testosterone also, apparently, alter the efficiency of the immune system and a number of other physiological processes. Hence, they suggested that exposure of the foetus to high levels of testosterone causes a constellation of effects. Geschwind and Galaburda (1987) have also argued that abnormally high levels of testosterone may cause "giftedness", and even that homosexuality results from effects of testosterone on brain lateralization and that is coupled with an immune system more susceptible to AIDS infection. This latter hypothesis is based on several assumptions and a rather convoluted path of reasoning. Firstly they believe, without convincing evidence of support, that male homosexuality depends on lower than normal levels of circulating free testosterone, and also that it results from stress during pregnancy. This stress is said to cause a transient increase in testosterone levels to be followed later by a rebound lowering of testosterone levels. The transient increase in testosterone, they hypothesise, causes increased "nonrighthandedness" in homosexuals and possibly an immunological condition more susceptible to autoimmune disease (pp. 175 of Geschwind and Galaburda, 1987).

There is no evidence from the human species to support these ideas, and the experimental data obtained from animals demonstrate clearly that such complex behaviours cannot be tied to a unitary cause of hormonal action.

CONCLUSIONS

The number of examples of both structural and functional laterality in nonhuman species is growing rapidly, and it is now clear that lateralization of brain structure and function developed very early in the course of evolution. Indeed, functional lateralization may have become an essential aspect of brain function not long after the brain became bilaterally duplicated in structure. It did not arise secondarily to shared tool use and handedness in humans, although these factors may subsequently have influenced the degree and nature of the laterality. Laterality in perceptual and cognitive processes appears to have been an antecedent to laterality of limb use in both birds and primates.

It is timely for psychologists concerned with understanding laterality in the human species to examine the data available in animals, not simply to find evidence for the evolutionary origins of laterality in humans, but also to discover the factors which influence the development of laterality. Experience has been shown to play an important role in the development of laterality in two species so far. The sex hormones also influence the development of asymmetry, but their role does not appear to be straightforward in the way postulated by some psychologists working with humans.

Laterality in the nervous system can occur in a number of different forms: structural and functional, at the population level and the individual level. Functional laterality may even change from 'moment-to-moment' as in the case of lateralized sleep in birds. A static view of laterality may have served a purpose while we were still in the phase of documenting the presence of asymmetries in different species, but laterality is a dynamic phenomenon varying with age, experience and the particular situation in which the animal finds itself. The studies using animals are providing a means to understand these dynamic processes in laterality.

REFERENCES

Adret, P. & Rogers, L.J. (1989). Sex difference in the visual projections of young chicks: A quantitative study of the thalamofugal pathway. *Brain Research, 478*, 59-73.

Andrew, R.J. & Brennan, A. (1983). The lateralization of fear behaviour in the male domestic chick: A developmental study. *Animal Behaviour, 31*, 1166-1176.

Andrew, R.J. & Brennan, A. (1984). Sex differences in lateralization in the domestic chick. *Neuropsychologia, 22*, 503-509.

Andrew, R.J. & Brennan, A. (1985). Sharply timed and lateralized events at time of establishment of long term memory. *Physiology & Behaviour, 34*, 547-556.

Andrew, R.J., Mench, J. & Rainey, C. (1982). Right-left asymmetry of response to visual stimuli in the domestic chick. In D.J. Ingle, M.A. Goodale & R.J.W. Mansfield (Eds.), *Analysis of visual behavior*, (pp. 197-209) Cambridge, MA: MIT Press.

Ball, N.J., Amlaner, C.J., Shaffery, J.P. & Opp, M.R. (1988). *Asynchronous eye-closure and unihemispheric quiet sleep of birds.* In W.P. Koella, H. Schulz, F. Obala & P. Visser (Eds.), *Sleep '86*, (pp. 27-28). Stuttgart, W. Germany: Verlag.

Bakalkin, G.Y., Tsibezov, V.V., Sjutkin, E.A., Veselova, S.P., Novikov, I.D. & Krivosheev, O.G. (1984). Lateralization of LH-RH in the rat hypothalamus. *Brain Research, 296*, 361-364.

Berrebi, A.S., Fitch, R.H., Ralphe, D.L., Denenberg, J.P., Friedrich, V.L. Jr., & Denenberg, V.H. (1988). Corpus callosum: Region-specific effects of sex, early experience and age. *Brain Research, 438*, 216-224.

Bianki, V.L. (1983). Simultaneous and sequential processing of information by different hemisphere in animals. *International Journal of Neuroscience, 22*, 1-6.

Bianki, V.L. (1988). *The right and left hemispheres of the animal brain, monographs in neuroscience, 3*, New York: Gordon & Breach.

Boxer, M.I. & Stanford, D. (1985). Projections to the posterior visual hyperstriatal region of the chick: An HRP study. *Experimental Brain Research, 57*, 494-498.

Bradshaw, J.L. & Nettleton, N.C. (1982). Language lateralization to the dominant hemisphere: Tool use, gesture and language in hominid evolution. *Current Psychological Reviews, 2*, 171-192.

Brookshire, K.H. & Warren, J.M. (1962). The generality and consistency of handedness in monkeys. *Animal Behaviour, 10*, 222-227.
Bullock, S.P. & Rogers, L.J. (1986). Glutamate-induced asymmetry in the sexual and aggressive behaviour of young chickens. *Pharmacology, Biochemistry & Behaviour, 24*, 549-554.
Cipolla-Neto, J., Horn, G. & McCabe, B.J. (1982). Hemispheric asymmetry and imprinting: The effect of sequential lesions of the hyperstriatum ventrale. *Experimental Brain Research, 48*, 22-27.
Collins, R.L. (1975). When left-handed mice live in right-handed worlds. *Science, 187*, 181-184.
Corballis, M.C. (1983). *Human laterality.* New York: Academic Press.
Cowan, W.M., Adamson, L. & Powell, T.P.S. (1961). An experimental study of the avian visual system. *Journal of Anatomy* (London), *95*, 545-563.
Denenberg, V.H. (1981). Hemispheric laterality and the effects of early experience. *The Behavioural and Brain Sciences, 4*, 1-21.
Denenberg, V.H. (1984a). Behaviour asymmetry. In N. Geschwind & A.M. Galaburda (Eds.), *Cerebral dominance: The Biological foundations* (pp. 114-133). Cambridge, MA: Harvard University Press.
Denenberg, V.H. (1984b). Effects of right hemisphere lesions in rats. In A. Ardila & F. Ostrosky-Solis (Eds.), *The right hemisphere: Neurology and neuropsychology* (pp. 241-262). New York: Gordon and Breach.
Denenberg, V.H., Rosen, G.D., Hofmann, M., Gall, J., Stockler, J. & Yutzey, D.A. (1982). Neonatal postural asymmetry and sex differences in rats. *Developmental Brain Research, 2*, 417-419.
Denenberg, V.H. & Yutzey, D.A. (1985). Hemispheric laterality, behavioural asymmetry and the effects of early experience in rats. In S.D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 109-133). New York: Academic Press.
Diamond, M.C. (1984). Age, sex, and environmental influences. In N. Geschwind & A.M. Galabarda (Eds.), *Cerebral dominance* (pp. 134-146). Cambridge, MA: Harvard University Press.
Diamond, M.C. (1985). Rat forebrain morphology: Right-left; male-female, young-old; enriched-impoverished. In S.D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 73-87). New York: Academic Press.
Ducker, G., Luscher, C. & Schultz, P. (1986). Problemlöseverhalten von Stieglitzen (*Carduelis carduelis*) bei 'manipulativen' Aufgaben. *Zoologisches Beitr., 23*, 377-412.
Friedman, H. & Davis, M. (1938). "Left-handedness" in parrots. *Auk, 80*, 478-480.
Frost, G.T. (1980). Tool behaviour and the origins of laterality. *Journal of Human Evolution, 9*, 447-459.
Gaston, K.E. & Gaston, M.G. (1984). Unilateral memory after binocular discrimination training: Left hemisphere dominance in the chick? *Brain Research, 303*, 190-193.
Gazzaniga, M.S. (1974). Cerebral dominance viewed as a decision system. In S.J. Dimond & J.G. Beaumont (Eds.), *Hemispheric function in the human brain* (pp. 367-382). London, UK: Elek Science.
Gazzaniga, M.S. & Le Doux, J.E. (1978). *The integrated mind.* New York: Plenum Press.
Geschwind, N. & Behan, P. (1982). Left-handedness: Association with immune disease, migraine and developmental learning disorder. *Proceedings of the National Academy of Science, USA, 79*, 5097-5100.
Geschwind, N. & Galaburda, A.M. (1987). *Cerebral lateralization; biological mechanisms, associations, and pathology.* Cambridge, MA: MIT Press.
Geschwind, N. & Levitsky, W. (1968). Human brain: Left-right asymmetries in temporal speech region. *Science, 461*, 186-187.
Glick, S.D. (1983). Cerebral lateralization in the rat and tentative extrapolations to man. In M.S Mysolobodsky (Ed.), *Hemisyndromes* (pp. 7-26). New York: Academic Press.
Glick, S.D. & Shapira, R.M. (1985). Functional and neurochemical mechanisms of cerebral lateralization in rats. In S.D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 157-183). New York: Academic Press.

Guiard, Y., Diaz, G. & Beaubaton, D. (1983). Left-hand advantage in right-handers for spatial constant error: Preliminary evidence in a unimanual ballistic aimed movement. *Neuropsychologia, 21*, 111-115.
Güntürkün, O. (1985). Lateralization of visually controlled behavior in pigeons. *Physiology and Behaviour, 34*, 575-577.
Güntürkün, O., Kesch, S. & Delius, J.D. (1988). Absence of footedness in domestic pigeons. *Animal Behaviour, 36*, 602-604.
Horn, G. (1985). *Memory, imprinting and the brain.* Oxford, UK: Oxford University Press.
Howard, K.J., Rogers, L.J. & Boura, A.L.A. (1980). Functional lateralization of the chick forebrain revealed by use of intracranial glutamate. *Brain Research, 188*, 369-382.
Kimura, D. (1979). Neuromotor mechanisms in the evolution of human communication. In H.D. Steklis & M.J. Raleigh (Eds.), Neurobiology of logic communication in primates (pp. 197-219). New York: Academic Press.
Levy, J. (1974). Psychobiological implications of bilateral asymmetry. In S. Dimond & J.G. Beaumont (Eds.), *Hemispheric Function in the Human Brain* (pp. 121-175). London, U.K.: Paul Elek.
Levy, J. (1979). Human cognition and lateralization of cerebral function. *Trends in the Neurosciences, 9*, 222-225.
MacNeilage, P.F., Studdert-Kennedy, M.G. & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences, 10*, 247-303.
McShane, S., Glaser, L., Greer, E.R., Hontz, J., Tong, M.F. & Diamond, M.C. (1988). Cortical asymmetry: A preliminary study; neuron-glia, female-male. *Experimental Neurology, 99*, 353-361.
Mench, J.A. & Andrew, R.J. (1986). Lateralization of a food search task in the domestic chick. *Behavioral and Neural Biology, 46*, 107-114.
Nordeen, E.J. & Yahr, P. (1982). Hemispheric asymmetries in the behavioral and hormonal effects of sexually differentiating mammalian brain. *Science, 218*, 391-394.
Nottebohm, F. (1971). Neural lateralization of vocal control in a passerine bird I: Song. *Journal of Experimental Zoology, 177*, 229-262.
Nottebohm, F. (1976a). Left hypoglossal dominance in the control of canary and white-crowned sparrow song. *Journal of Comparative Physiology, 108*, 171-192.
Nottebohm, F. (1976b). Phonation in the orange-winged amazon parrot, *Amazona amazonica. Journal of Comparative Physiology, 108*, 157-170.
Nottebohm, F. (1977). Asymmetries in neural control of vocalisation in the canary. In S. Harnard, R.W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (Eds.), *Lateralisation in the Nervous System* (pp. 23-24). New York: Academic.
Nottebohm, F. (1987). Plasticity in adult avian central nervous system: Possible relation between hormones, learning, and brain repair. In V.B. Mountcastle, F. Plum & S.R. Geiger (Eds.), *Handbook of physiology V*; Section 1. *The nervous system* (pp. 85-108). Maryland: American Physiological Society.
Nottebohm, F. (1989). From bird song to neurogenesis. *Scientific American*, Feb., 55-61.
Peterson, M.R., Beecher, M.D., Zoloth, S.R., Moody, D.B. & Stebbins, W.C. (1979). Neural lateralization of species-specific vocalisations by Japanese macaques (*Macaca fuscata*). *Science, 202*, 324-327.
Phillips, R.E. & Yongren, O.M. (1986). Unilateral kainic acid lesions reveal dominance of right archistriatum in avian fear behavior. *Brain Research, 377*, 216-220.
Robinson, T.E., Becker, J.B. & Camp, D.M. (1983). Sex differences in behavioural and brain asymmetries. In M.S. Myslobodsky (Ed.), *hemisyndromes* (pp. 91-128). New York: Academic Press.
Rogers, L.J. (1981). Environmental influences on brain lateralization. *The Behavioural and Brain Sciences. 4*, 35-36.
Rogers, L.J. (1982). Light experience and asymmetry of brain function in chickens. *Nature, 297*, 223-225.
Rogers, L.J. (1986). Lateralization of learning in chicks. *Advances in the Study of Behaviour, 16*, 147-189.
Rogers, L.J. (1990a). Light input and the reversal of functional lateralization in the chicken brain. *Behavioural Brain Research, 38*, 211-221.

Rogers, L.J. (1990b). Development of lateralisation. In R.J. Andrew (Ed.), *Neural and Behavioural Plasticity: The Use of the Domestic Chick as a Model*, in press, Oxford, U.K.: Oxford University Press.

Rogers, L.J. & Anson, J.M. (1979). Lateralization of function in the chicken forebrain. *pharmacology, Biochemistry and Behavior, 10*, 679-686.

Rogers, L.J. & Sink, H.S. (1988). Transient asymmetry in the projections of the rostral thalamus to the visual hyperstriatum of the chicken, and reversal of its direction by light exposure. *Experimental Brain Research, 70*, 378-384.

Rogers, L.J. & Workman, L. (1989). Light exposure during incubation affects competitive behaviour in domestic chicks. *Applied Animal Behaviour Science, 23*, 187-198.

Rogers, L.J., Zappia, J.V. & Bullock, S.P. (1985). Testosterone and eye-brain asymmetry for copulation in chickens. *Experientia, 41*, 1447-1449.

Rose, S.P.R. & Csillag, A. (1985). Passive avoidance training results in lasting changes in deoxyglucose metabolism in left hemisphere regions of the chick brain. *Behavioral and Neural Biology, 44*, 315-324.

Rosen, G.D., Berrebi, A.S., Yutzey, D.A. & Denenberg, V.H. (1983). Prenatal testosterone causes shift of asymmetry in neonatal tail posture of the rat. *Developmental Brain Research, 9*, 99-101.

Rosen, G.D., Finklestein, S., Stoll, A.L., Yutzey, D.A. & Denenberg, V.H. (1984). Neonatal tail posture and its relationship to striatal dopamine asymmetry in the rat. *Brain Research, 297*, 305-308.

Ross, D.A., Glick, S.D. & Meibach, R.C. (1981). Sexually dimorphic brain and behavioral asymmetries in the neonatal rat. *Proceedings of the National Academy of Science,* USA, *78*, 1958-1961.

Schwarting, R., Nagel, J.A. & Huston, J.P. (1987). Asymmetries of brain dopamine metabolism related to conditioned paw usage in the rat. *Brain Research, 471*, 75-84.

Sherman, G.A., Garbanati, J.A., Rosen, G. D., Yutzey, D.A. & Denenberg, V.H. (1980). Brain and behavioral asymmetries for spatial preference in rats. *Brain Research, 192*, 61-67.

Stewart, M.G., Rose, S.P.R., King, J.S., Gabbott, P.L.A., & Bourne, R. (1984). Hemispheric asymmetry of synapses in the chick medial hyperstriatum ventrale following passive avoidance training: A stereological investigation. *Developmental Brain Research, 12*, 261-269.

Walker, S.F. (1980). Lateralization of functions in the vertebrate brain: A review. *British Journal of Psychology, 71*, 329-367.

Ward, J.P. (1990). Prosimians as animal models in the study of neural lateralization. In F.L. Kitterle (Ed.), *Cerebral laterality: Theory and research. The Toledo Symposium*, in press, Hillsdale, N.Y.: Lawrence Erlbaum Press.

Warren, J.M. (1958). The development of paw preferences in cats and monkeys. *Journal of Genetic Psychology, 93*, 229-336.

Warren, J.M. (1980). Handedness and laterality in humans and other animals. *Physiological Psychology, 8*, 351-359.

Workman, L. & Andrew, R.J. (1986). Asymmetries of eye use in birds. *Animal Behaviour, 34*,1582-1584.

Zappia, J.V. & Rogers, L.J. (1983). Light experience during development affects asymmetry of forebrain function in chickens. *Developmental Brain Research, 11*, 93-106.

Zappia, J.V. & Rogers, L.J. (1987). Sex differences and reversal of brain asymmetry by testosterone in chickens. *Behavioural Brain Research, 23*, 261-267.

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A PERCEPTUAL-MOTOR MODEL FOR SPATIAL ORIENTATION OF SHAPES

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ABSTRACT: A model will be presented in which mirror image confusion is employed as an example of perception of shape orientation, occurring as a result of evolutionary change in vision and movement. In the most primitive condition, vertical and horizontal coordinates are absent and shapes are equivalent in terms of orientation. In this condition directionality in external space is not objectified and movement is reflexively toward or away from the visual target. In the second condition, only the horizontal axis is present. Changes in orientation from upward to downward are perceptually salient. Quadrupedal movement patterns and locomotion across land, dominated by the horizon, are associated with the evolution of a mammalian eye with enhanced acuity across the vertical axis. Vertical mirror image confusion ceases to exist. In the third condition, the vertical axis appears. Factors in primate evolution associated with the appearance of enhanced acuity along these visual axes are related to perception of lateral rotations. In the fourth condition, upright posture and development of lateral bias in eye movement are related to the human proclivity to differentiate right and left orientation of shapes while exhibiting increased difficulty in tasks that involve changes in the vertical orientation. Thus structural changes in evolution associated with posture and movement are demonstrated to account for differences in perceptual responses to orientation of shapes.

KEY WORDS: Perceptualmotor; Shape orientation; Evolution; Laterality; Posture.

Mirror image confusion is the tendency to have difficulty in learning the difference between shapes rotated 180 degrees on their own axes. Lateral mirror images are asymmetrical shapes rotated across their vertical axes, while vertical mirror images are shapes rotated on their horizontal axes. The perceptual phenomenon of lateral mirror image confusion (difficulty with shapes rotated left or right rather than up or down) is of interest in the study of the evolution of visually guided behavior because lateral mirror image confusion is evident in many species, including octopus (Sutherland, 1957), rats (Kinsbourne, 1971), cats (Parriss, 1964), ferrets (Wight, Milliken, & Ward, 1988), bushbabies (Sanford & Ward, 1986), and monkeys, (Riopelle, Rahm, Itiogawa & Draper, 1964), as well as in human children (Bryant, 1969). It is notably absent in most intact human adults. There have been attempts to explain the absence of lateral mirror

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image confusion in humans in terms of their learned ability to read left to right and thus make discriminations based on verbal rules differentiating right from left facing characters (b from d). More neurobehaviorally oriented explanations account for lateral mirror image confusion, or its absence, in terms of cerebral asymmetries, (see Corballis, 1983). However, it is of interest to think of mirror image confusion as an example of the perception of orientation in extrapersonal space, and consider how and why this sort of perceptual response might change along evolutionary lines.

Over the past few years there has been a renewed interest in motor theories about perception (see Schierer, 1987). Recent investigations with human subjects have demonstrated the role of movement bias and postural adjustment in visual judgment of line length and directionality (Coren, 1986), circle size (Coren, Bradley, Hoeing, & Girgus, 1975), shape identification (Rock, 1974), and tactuospatial learning (Ward, Alvis, Sanford, Dodson, & Pusakulich, 1989). From a comparative point of view, one is compelled to wonder how changes in sensory and motoric factors, under the pressures of environmental adaptation, might influence the nature of an animal's perceptual world. In this paper, we will present a model, based upon data relevant to mirror image confusion. This model demonstrates how the structure of the visual apparatus as well as the structure of the body itself might determine factors relative to how objects are perceived to be oriented in space.

The first step in this model, depicted in Figure 1a, is a blank field. Notably absent are the axes marking any vertical or horizontal coordinates, so that this two dimensional field is essentially directionless. This is the baseline of the model. If the letters b, d, p, q, representing visual targets, are superimposed on this field, there would be no way to discriminate them visually. In a directionless field they would be identical.

Mach (1987) long ago observed that a perfectly symmetrical organism would have total mirror image confusion. We have no data concerning such an organism. What needs to be considered is the nature of the living animal's perceptual field relative to the salience of orientation of objects within that field. A simple example is found in the visually guided behavior of the salamander. If the eyeball of the salamander is rotated 180 degrees on its optic axis, it will heal in position. The retina is then turned upside down and right to left. The result is that all visuo-motor responses toward prey are reversed. It will continue this backward behavior until starvation (Sperry, 1943). The relationship between the salamander's visual space and the environmental space in which it operates is fixed. Right, left, above or below have no objective significance, since as demonstrated experi-

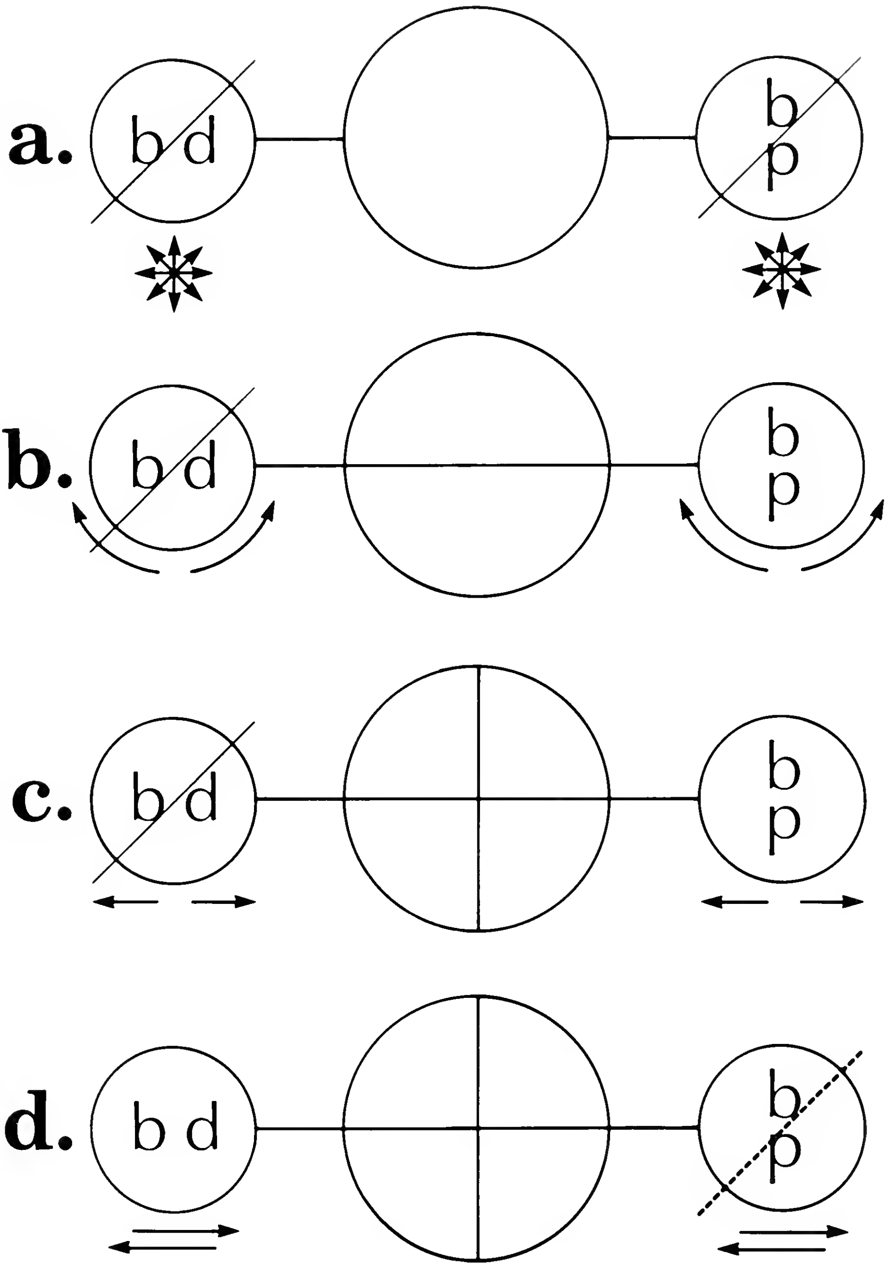

FIGURE 1. Diagrammatic representation of the model. Central circles represent visual fields with horizontal and vertical meridians indicated. Mirror image pairs are within peripheral circles for each visual field. Pairs which cause confusion are marked with cross bars. Dashed lines indicate a partial or questionable state. Arrows represent directionality in inspection.

mentally, its responses are determined by stimulation of retinal points, not by its actual relationship to objects in space. Another example is found in an animal that normally does show mirror image confusion, for lateral but not up-down rotations (Sutherland, 1957). The octopus has a nervous system that is radially symmetrical. Because it feeds while clinging to objects in the water, whether upside down or horizontally positioned, the octopus is often in a strange relation to gravity. To compensate for its seeming disregard of up and down, the octopus eye is structured so that it rotates relative to gravitational down. It has been demonstrated that if the vestibular pathway controlling eye movement is lesioned, the eye no longer responds as described and the octopus loses all learned ability to make a vertical mirror image discrimination (Young, 1971). In the baseline condition of our model, as for the lesioned octopus, right, left, up and down are equivalent. Both lateral and vertical mirror image confusion are the rule.

The second condition, seen in Figure 1b, represents a visual field with only one axis, the horizontal meridian. If the letter b is rotated 180 degrees across the horizontal meridian, it becomes p. When the difference between b and p is appreciated, a vertical mirror image discrimination has been made. Thus an organism to whom up and down, top and bottom of objects in the environment are behaviorally meaningful would implicitly structure visual space about this axis. But what is the behavioral significance of the horizontal axis? When an animal moves on four legs across the land, following and watching its prey or its enemies, it is dependent for survival upon their movement patterns as much as its own. Changes in landscape are critical for movemer The horizon itself is the most basic referent for vision. The salience oi the horizontal plane to vision is imprinted even in the structure of the eye. For example, the Mongolian gerbil, a small rodent living in a flat, arid environment, has its highest acuity along the horizontal axis of the retina (Baker & Emerson, 1983). If such a case is considered to be a minimal structural condition for the visual adaptation of a free-ranging ground mammal to its environment, it is little wonder that vertical mirror image confusion would not exist at this level.

But what about lateral mirror image confusion? In Figure 1b, where there is absence of a vertical meridian, if b and d are represented, they are the same, since d is simply b rotated on its own vertical axis. If lateral mirror image confusion is a result of the absence of a vertical axis in the perceptual field, as the model would have it, what would we need to consider in the behavior of animals to support the model?

Although much is known about visual capacities of animals, less has been said about how they inspect objects in order to learn some-

thing about them. It is important to consider the structure of the animal as well as the behavior. For most non-primate mammals, the eyes are laterally placed, offering a wide breadth of view. With foveal vision absent, lateral excursion of eye movement is limited, and movement of the head, as well as movement in space, takes precedence. The non-primate, without hands to manipulate objects for inspection or to bring them closer to view, is more dependent upon its own movement toward and around objects as an inspection strategy. Our own observations are that while dogs or cats (predators) will quietly gaze at an object awaiting its movement, they inspect by such behaviors as headcocking, or moving about the object of interest. Rats, learning to discriminate two dimensional forms from a distance, make repetitive, back and forth movements before the task is achieved. The tree shrew, in the same situation, weaves wild figure eights with its body as learning is accomplished. In short, when visual inspection is tied closely to movement of the body, the right and left halves of space relative to some critical axis are perhaps not so important for visual learning. For a quadrupedal animal the plane of movement is predominantly on the horizontal. If one moves around the b and the d horizontally, they become interchangeable. If one moves around a saber toothed tiger, he is the same tiger on either side. If on the other hand, his feet are in the air, or worse, if yours are, the world begins to look a bit different. In Figure 1b, lateral mirror image confusion exists, but vertical mirror image confusion does not.

In the third condition, Figure 1c, the vertical axis appears. Now space is divided into right and left halves in which the d points left but if rotated on the vertical axis becomes b, pointing right. Again, structural considerations are important in applying the model to animal vision. Both the evolution of the eye as well as changes in posture and limb use separate the primate from the non-primate quadruped. In primates, who have enhanced specialization of central vision, the retinal areas of sharpest acuity occur along both the horizontal and vertical axes of visual space (Simeonova & Vassilev, 1985; Vandenbusshe & Orban, 1983). Thus, this condition can be thought of as representing a primate visual field. Wight et al (1988) have pointed out that the significance of the vertical meridian in vision appears to increase in the primate order as bipedalism begins to appear in mammals. It is an interesting thought that as the neuraxis becomes more vertically oriented, as the upright posture in locomotion evolves, the retinal structure also develops in such a way as to fine tune to the vertical dimension of space. As the forelimbs are freed from the reflexive constraints of locomotion, they become increasingly independent from each other. Also, with the evolution of the hand, the differentiation of the two halves of the body along the neuraxis give the

right and left halves of internal space a behavioral significance to the primate that is lacking in the quadruped. Thus, perception of internal space, the division of the body into distinct and independent halves along the neuraxis, is reflected by a perception of external space in which right and left halves also exist visually.

But how do these evolutionary changes relate to the perception of orientation and to mirror image confusion? Once the vertical axis is established, the lateral mirror images b and d can be inspected in one of two ways, medially to laterally, as diagramed in Figure 1c, or from one pole of the horizontal axis to the other as in Figure 1d, right to left or left to right. The perceptual result is quite different, for with medial to lateral inspection b continues to equal d. It is only with a consistent lateral bias in the sequence of movement that lateral mirror image confusion disappears. Let us assume that the medial to lateral inspection represents the condition found in such primitive primates as the bushbaby, or the monkey, who can learn a lateral mirror image discrimination but with considerable difficulty (Sanford & Ward, 1986) while the right to left, left to right sequence represents the adult human who makes these discriminations easily. Prosimians and simians show far less independent use of each hand than humans. They also utilize the four limbs in locomotion such that bilaterally symmetrical or coordinated movements occur more frequently. For completely bipedal man with a highly independent use of two hands, there is a significant increase in movements not coordinated toward and away from the midline axis of the body. Thus the internal representation of the right and left halves of space gain increasing importance.

A second factor related to visual and somatic structure is equally important. In non-human primates, lateral excursion of the eyes is much less than for humans. Consequently, scanning across the visual field for the non-human primate is more dependent upon moving the head, an activity directed away from the midline of the body, medial to lateral. For humans, eye movements clearly exhibit a lateralized directional bias for inspection. Inspection of a complex visual array begins by entering the target on the left and moving rightward (Standing, Conezio, & Haber, 1970). In keeping with our model this consistent bias in sweep differentiates primates who show lateral mirror image confusion from those who do not. A medial to lateral head movement is the mode for the more primitive primates and possibly for children (Gesell & Ames, 1947; Coren, Porac, & Duncan, 1981). For humans, the lateralized scan, facilitated by wide lateral excursion of the eyes, promotes a consistently directional eye movement sequence. In fact, it has been demonstrated that individuals with visuospatial dyslexia, who tend to reverse words and letters, like a child learning to read, often show unusually erratic eye movements

while reading (Lesévre, 1968; Zangwill & Blakemore, 1972), and have difficulty tracking right-left or left-right light pattern sequences (Pavlidis, 1981).

Non-human primates, with a more vertical neuraxis than other mammals, do, like quadrupeds, exhibit lateral mirror image confusion, but, according to our model, for a different reason and possibly to a lesser degree. Bipedal man does not. But as the vertical axis gains salience, there appears to be a perceptual trade-off. This condition is represented in Figure 1d. It appears that humans, unlike any other mammals for whom data exists, suffer from vertical mirror image confusion. Rock (1974), has demonstrated that while subjects were easily able to identify familiar shapes, such as a map of Africa, as flipped from right to left, when the same map was turned upside down, it was not recognized. He attributed this to a tendency to assign a natural base to objects. Using a long series of abstract designs with no semblance of a natural base, we have found that although right-left reversals were recognized (although with some difficulty), vertical rotations were significantly more difficult (Sanford, 1986). This is not the case in any data from studies of animals or children in which the vertical rotation is used as a comparison, but supports data which shows that adult human subjects are slower to respond when differentiating the poles of horizontal axes (east verses west) than those of the vertical (north verses south) (Scholl & Egeth, 1981).

In summary, a model in which mirror image confusion has been presented, as an example of perception of shape orientation, occurs as a result of evolutionary change in vision and movement. In the most primitive condition, vertical and horizontal coordinates are absent and shapes are equivalent in terms of orientation. In this condition, directionality in external space is not objectified and movement is reflexively toward or away from the visual target. In the second condition, only the horizontal axis is present. Changes in orientation from upward to downward are perceptually salient. Quadrupedal movement patterns and locomotion across land, dominated by the horizon, are associated with the evolution of a mammalian eye with enhanced acuity across the vertical axis. Vertical mirror image confusion ceases to exist. In the third condition, the vertical axis appears. Factors in primate evolution associated with the appearance of enhanced acuity along these visual axes are related to perception of lateral rotations. In the fourth condition, upright posture and development of lateral bias in eye movement are related to the human proclivity to differentiate right and left orientation of shapes while exhibiting increased difficulty in tasks that involve changes in the vertical orientation. Thus structural changes in evolution associated with posture and movement are demonstrated to account for differences in perceptual responses to orientation of shapes.

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REFERENCES

Baker, A. G., & Emerson, V. F. (1983). Grating acuity of the Mongolian gerbil (*Meriones unguiculatus*). *Behavioral and Brain Research, 8*, 195-210

Bryant, P. E. (1969). Perception and memory of the orientation of visually presented lines by children. *Nature, 224*, 1331-1332.

Corballis, M. C. (1983). *Human laterality.* New York: Academic Press.

Coren, S. (1986). An efferent component in the visual perception of direction and extent. *Psychological Review, 93*, 391-410.

Coren, S., Bradley, D. R., Hoeing, P., & Girgus, J. S. (1975). The effect of smooth tracking and saccadic eye movements on the perception of size: The shrinking circle illusion. *Vision Research, 15*, 49-52.

Coren, S., Porac, C., & Duncan, P. (1981). Lateral preference behaviors in preschool children and young adults. *Child Development, 52*, 443-450.

Gesell, A. & Ames, L. B. (1947). The development of handedness. *Journal of Genetic Psychology, 70*, 155-175.

Kinsbourne, M. (1971). Discrimination of orientation by rats. *Psychonomic Science, 22*, 50.

Lesévre, N. (1968). L'organization du regard chez enfants d'age scholaire lecteurs normaux et dyslexiques (etude electroculoographique). *Revue de Neuropsychiatrie Infantile, 16*, 323-349.

Mach, E. (1987). *The analysis of sensations.* Chicago: Open Court.

Parriss, J. R. (1964). A technique for testing cat's discrimination of differently oriented rectangles. *Nature, 202*, 771-773.

Pavlidis, G. (1981). Do eye movements hold the key to dyslexia? *Neuropsychologia, 19*, 57-64.

Riopelle, A. J., Rahm, V., Itiogawa, N., & Draper, W. A. (1964). Discrimination of mirror image patterns by rhesus monkeys. *Perceptual and Motor Skills, 19*, 383-389.

Rock, I. (1974). The perception of disoriented figures. In R. Held (Ed.), *Image, object, and illusion.* San Francisco: W. H. Freeman.

Sanford, C. G. (1986). Recognition of geometric figures as a function of orientation, familiarity, and context. Unpublished doctoral dissertation, Memphis State University, Memphis, Tennessee, USA.

Sanford, C. G. & Ward, J. P. (1986). Mirror image discrimination and hand preference in the bushbaby (*Galago senegalensis*). *The Psychological Record, 36*, 439-449.

Schierer, W. L. (1987). Motor theories of cognitive structure: A historical review. In W. Prinz & A. F. Sanders (Eds.), *Cognitive and motor processes.* Berlin, Heidelberg: Springer-Verlag.

Sholl, M. & Egeth, H. E. (1981). Right-left confusion in the adult: A verbal labeling effect. *Memory and Cognition, 9*, 339-350.

Simeonova, B. & Vassilev, A. (1985). Perception of line orientation in the center and periphery of the visual field. *Acta Psychologia Pharmacologia Bulgaria, 11*, 3-10.

Sperry, R. W. (1943). Effect of 180 degree rotation of the retinal field on visuomotor coordination. *Journal of Experimental Zoology, 92*, 263-279.

Standing, L., Conezio, J., & Haber, R. N. (1970). Perception and memory for pictures: Single-trial learning of 2500 visual stimuli. *Psychonomic Science, 19*, 73-74.

Sutherland, N. S. (1957). Visual discrimination of orientation and shape by Octopus. *Nature, 179*, 11-13.

Vandenbusshe, E. & Orban, G. A. (1983). Meridional variation in the line orientation discrimination of the cat. *Behavioral and Brain Research, 9*, 237-256.

Ward, J. P., Alvis, G. R., Sanford, C. G., Dodson, D. L., & Pusakulich, R. L. (1989). Qualitative differences in tactuo-spatial motor learning by left-handers. *Neuropsychologia, 27*, 1091-1099.

Wight, R., Milliken, G., & Ward, J. P. (1988). Assessment of visual acuity, the oblique effect, and the lateral mirror-image confusion effect in the ferret (*Mustela putorius furo*). *International Journal of Comparative Psychology, 1*, 254-267.

Young, Z. G. (1971). The anatomy of the nervous system of *Octopus vulgaris*. Oxford: Clarendon Press.

Zangwill, O. L. & Blakemore, C. (1972). Dyslexia: Reversal of eye movements during reading. *Neuropsychologia, 10*, 371-373.

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LATERAL ASYMMETRIES IN HUMAN EVOLUTION

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ABSTRACT: Lateral asymmetries are not confined to humans. Palaeozoic trilobites and calcichordates are now known to have been asymmetrical; song control in passerines is vested in the left cerebral hemisphere; learning which is lateralized to the left forebrain of chicks includes imprinting, visual discrimination learning and auditory habituation, while responses to novelty, attack and copulation are activated by the right; in rats the right hemisphere is involved in emotional behavior and spatial discriminations, and there are numerous other behavioral, anatomical and pharmacological asymmetries; the left hemisphere of the female mouse is superior at processing its pups' calls, and there are reports of behavioral asymmetries in impala, cats and dogs. Anatomical asymmetries in the primate brain, from monkeys upwards, are matched by increasing evidence of behavioral asymmetries in visual pattern discrimination, discrimination of species-specific calls, and handedness. We discuss the interaction of preexisting behavioral and brain asymmetries with the evolution in hominids of an upright bipedal posture and tool use, and the origins of language, and conclude that there may be a continuity with earlier species of our two most obvious asymmetries, language lateralization and hand preferences. There may be an ancient left-brain specialization for sensory and motor discrimination learning, which is complemented by a relegation to the right of primitive spatial and emotional functions.

Most of us are right handed (dextral) and left-hemisphere (LH) dominant for language (Bradshaw & Nettleton, 1983). The two sides of the face rarely are left-right symmetrical, as can be seen if we create photographic composites of the two left (L⅃) or right (RЯ) halves. Moreover the left side of the face may express emotions more strongly than the right, due probably to its more direct access to the right hemisphere (RH), known to be involved in the mediation of emotions (Borod & Koff, 1984). Conversely the right side of the mouth may produce earlier, and larger, articulatory movements during speech than the left (Wolf & Goodale, 1987) again due to its more direct access to the LH. If male, the left testicle usually depends lower, as Greek sculptors knew 2,500 years ago (McManus, 1976). However we now know that many nonhuman species are also laterally asymmetrical, due ultimately perhaps to the chirality (handed-

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ness) of organic sugars, amino acids, and even the asymmetrical arrangement of the four bonds of the carbon atom. Thus virtually all the amino acids which constitute proteins are left handed, while the progenitor nucleotides in nucleic acids are correspondingly right handed. Even the weak nuclear interaction in physics contains a chiral bias; thus electrons emitted during the β decay of cobalt-60 are predominantly left handed, in terms of the preferred alignment of the particle's spin with its direction of motion. Such physical forces, acting through biochemistry, may have determined cytoplasmic asymmetries in the cell in terms of an asymmetric arrangement of fibrils formed by structural proteins. These would determine the directional beat of cilia and ultimately perhaps even the structure and function of the nervous system (Geschwind & Galaburda, 1985).

According to Jeffries and Lewis (1978), the most primitive fossil chordates (calcichordates, occurring during the Cambrian epoch) were very asymmetric in the head region. More advanced mitrate calcichordates, foreshadowing vertebrates, became almost externally symmetrical, while retaining an internal asymmetry. Whether or not true vertebrates did arise from calcichordates, it is noteworthy that the habenular nuclei of the frog, newt and eel thalamus tend to be more "lobate" on the left (Braitenberg & Kemali, 1970), and the anatomically-connected parietal eye of the lizard exhibits similar asymmetries (Engbreston, Reiner & Brecha, 1981). In the domestic chick, at least in males, the medial habenular nucleus (which responds to testosterone) is larger on the right (Gurusinghe & Ehrlich, 1985). In rabbit, rat, mouse and cat the RH is larger (Kolb, Sutherland, Nonneman & Whishaw, 1982). Behavioral asymmetries may even occur as early as the Paleozoic. Thus healed scars on Paleozoic trilobites attributed to sublethal predation are found more frequently on the right side, suggesting that predators prefer to attack in a specific direction, or that the arthropod victims tended to face their attackers in a specific (i.e. asymmetric) orientation (Babcock & Robinson, 1989). So far this is the earliest evidence of behavioral asymmetry in the fossil record.

Until recently, only humans were thought to exhibit motor (handedness) or cognitive (e.g. language) asymmetries. Asymmetry was even thought to be disadvantageous, in that it might be more useful to be able to generalize between events occurring on either side of the body, rather than to distinguish between them. (We shall however shortly see that asymmetries may permit the development of spatial or directional maps where directional turns to left or right could be important.) While manipulative dexterity has reached an evolutionary peak in our own species, it is nevertheless well developed in rodents, racoons, cats, bears, monkeys and apes. Such animals have long been known to possess strong and stable hand or paw pref-

erences, but were thought not to be biased at the population level. Innate individual differences seemed to be relatively resistant to imposed environmental biases; nor did selective breeding alter the 50/50 distributions of right and left pawed mice in later generations (Collins, 1977). However we shall examine the very recent evidence that monkeys are biased with respect to handedness at a population level, that the brains of apes exhibit asymmetries similar to our own, and that a host of mammals and birds show striking sensory and motor asymmetries at the population level.

STUDIES WITH BIRDS

There is a striking functional asymmetry in the vocal control of song in various passerines (see e.g. Nottebohm, 1979). In adult male canaries, section of the right hypoglossal nerve (supplying the right side of the syrinx or vocal organ) has relatively little effect upon song, while section of the left side leads to elimination of most of the song's components. Within the brain itself, lesions of the caudal nucleus of the hyperstriatum ventrale on the left has a similarly detrimental effect (unlike the normal vertebrate pattern of limb control, but like the olfactory sense, the entire system is nondecussatory or uncrossed). Damage to the left side in young chaffinches, or in canaries early in the season before they commence their annual learning of a new repertoire, may release the right from left-side inhibition. Thus the right may be permitted to take over song function, just as in very young children the RH can take over speech functions from a damaged LH (Goodman & Whitaker, 1985). However McCasland (1987), employing both bilateral brain lesions and peripheral disruptions of the vocal apparatus, was unable to demonstrate any functional asymmetry, and concluded that both hemispheres and syringeal halves normally make similar contributions to song production.

In parrots there seems to be bilateral representation of the vocal apparatus, despite their ability to learn and reproduce complex sounds. However many species are left footed for food manipulation (Rogers, 1980), suggesting an analogy (but not a homology) with humans. (Indeed some Australian species are predominantly *right* footed.) Moreover as there is no evidence of a correlation between limb and vocal asymmetries, we should be wary of arguments that humans need unilateral control of a single set of articulators to avoid competition and e.g. stuttering (Corballis, 1981; Falk, 1987). Nevertheless it is intriguing (Walker, 1987) that the right branch of the recurrent laryngeal nerve which innervates the intrinsic muscles of the human larynx is the shorter. We might then require unilateral control (by the contralateral LH?) in the presence of two routes of

different lengths which could otherwise lead to synchronization problems. (MacNeilage, Studdert-Kennedy & Lindblom, 1988, however, ask why an earlier-arriving subsystem should thereby acquire a processing advantage, and why differences in pathway lengths should lead to problems in coordination; they also note that length differences seem to be exactly compensated for by differences in diameter, thus negating any differences in arrival times.) Finally, to return to avian foot asymmetries, Güntürkün, Kesch and Delius (1988) report that, like parrots, goldfinches are asymmetrical in foot usage; however they exclusively use the *right* foot to release catches.

In the bird visual system, there is complete decussation, so that occlusion of one eye permits direct stimulation of the ipsilateral hemisphere via the opposite eye. Moreover injection of e.g. amnesic agents into one or the other side of the brain can unilaterally suppress memory formation. Rogers (1980) reviews the earlier evidence that learning which is lateralized to the left forebrain of domestic chicks includes imprinting, visual discrimination learning, auditory habituation and attention switching. The left forebrain is more likely to activate a pecking response, and also to inhibit it when no longer rewarded, while responses to attack, novelty and copulation tend to be activated by the RH and inhibited by the LH. However, the sexes differ in how brain lateralization is manifested, which itself is subject to further developmental changes. Thus only males, and only for the first two weeks after hatching, exhibit structural asymmetries in certain thalamofugal visual pathways (Adret & Rogers, 1989). In females, there is no such *structural* asymmetry, though there is some evidence of *functional* asymmetry in visual discrimination learning in female chicks during the first few days post-hatch. While both sexes exhibit similar asymmetries with respect to learning, attack, novelty and copulation (see above), they can only be demonstrated, in young males, by direct testing via one or other eye; in females, however, as in males, they can be demonstrated by chemical inactivation of one or other hemisphere. These asymmetries may be important for the early imprinting process, (and indeed Horn and Johnson, 1989, describe functional asymmetries between the left and right hyperstriatum ventrale in short and long term storage functions in the acquisition of visual imprinting). Moreover testosterone can even reverse asymmetries in male chicks, and light seems to play a crucial role. Thus, *in ovo*, just before hatching, the chick's head is turned up on its left shoulder, shielding the left eye and ear, and only the right eye and ear can receive sensory inputs to activate the LH. Indeed consistent lateralization at a population level may fail to appear if the eggs are protected from light and sound before hatching (Rogers, 1980, 1982), though at the level of the individual chick the brain remains (inconsistently) asymmetric. (A somewhat similar argument, position *in*

utero, has been developed to explain head-turning reflexes in human neonates, which could possibly underlie subsequent hand preferences, Turkewitz, 1977.) Thus light determines the *direction*, not the *presence* of asymmetries, and indeed if light is shone prior to hatching into the normally occluded left eye, with occlusion now of the normally exposed right eye, the direction of asymmetries, structural and behavioural, reverses. Genes, hormones and environmental influences all therefore contribute to the manifestation of lateral asymmetries. The same is probably true with humans.

Andrew and colleagues (Andrew, 1983, 1988; Andrew, Mench & Rainey, 1982) extended Rogers' conclusions, though their conclusions were frequently modified by complex sex and developmental differences. They showed that untreated chicks learn simple visual discriminations faster via the right eye/LH system (and see also Zappia and Rogers, 1987); with left eye/RH input, fear responses increased. The right eye/LH system may habituate faster to novelty, and be better able to withold responses to irrelevant stimuli by controlling lower-level instinctive emotional responses, than the left eye/RH system. The latter, according to Andrew, may have a special interest in spatial positioning and emotional reactivity; it may act as a passive observer, while the right eye/LH system may actively catergorize and select important stimuli for sequential responding. Such a model, which can be extended to cover LH mediation of song control in passerines (above) has obvious affinities with the idea of an analytic/holistic processing dichotomy in humans (Bradshaw & Nettleton, 1981). Indeed Andrew and Brennan (1985) showed that while birds using the left-eye/RH system were less competent than those using the right eye/LH system at "analytic" tasks of discriminating between categories of peckable objects, they were much better at generalizing aversive training to ill-tasting beads of different colors. There may also be a similarity with Bianki's (1983) findings with the formation, generalization and specialization of conditioned reflexes in rats while one or other cerebral hemisphere was chemically inactivated; he claims that synthetic generalizations proceeds more strongly in the RH, while analytic specialization proceeds better in the LH. Stewart, Rose, King, Gabbott and Bourne (1984) used acquisition of a similar passive avoidance task (withholding pecking of bright beads with unpleasant taste) to study the effects upon synapses in the medial hyperstriatum ventrale. In terms of the number of vesicles per synapse, values on the left side of trained chicks massively exceeded those on the right. This structure may also be asymmetrically involved in imprinting (Bradley, Horn, & Bateson, 1981). Indeed just as in the chick, use of the right eye/LH system in pigeons may lead to better visual discriminations (Güntürkün & Kesch, 1987). Finally Vallortigara, Zanforlin and Caillotto (1988) showed that male chicks

demonstrated faster discrimination learning when a critical box is placed to the right rather than the left in a T maze.

STUDIES WITH RODENTS

Studies with rats have recently demonstrated some of the most striking morphological, pharmacological and behavioural asymmetries. However mice, while possessing strong individual paw preferences, nevertheless split 50/50 at the population level even after prolonged selective breeding (Collins, 1985). However, just as with humans (Bryden & Steenhuis, 1987), breeding may selectively alter *strength* of pawedness, and likewise female mice turn out to be the more lateralized in motor preferences. (In humans, at the *cognitive* as opposed to the *motor* level, e.g. with respect to language, females may be *less* lateralized, McGlone, 1980.) Mice bred for stronger behavioural asymmetries also possess more asymmetrical and heavier brains, and tend to be more reproductively successful and masculinized (Ward & Collins, 1985, and cf. the role of testosterone in human cerebral asymmetry, Geschwind & Galaburda, 1985). Furthermore, more lateralized rats may learn spatial responses faster (Zimmerberg, Strumpf, & Glick, 1978; Camp, Therrien, & Robinson, 1981).

The neocortex of the RH of New Zealand black mice is larger than the left (Rosen, Sherman, Mehler, Emsbo, & Galaburda, 1989), and the rat likewise exhibits pronounced brain asymmetries (Heine & Galaburda, 1986), though there are considerable sex differences (Diamond, 1984, 1985). Lesions to the RH, rather than the LH, may cause (transient) changes in catecholamine levels and emotional behaviour (Dewberry, Lipsey, Sood, Moran & Robinson, 1986). Indeed RH ablations may even lead to immune suppression in female rats, apparently mediated via prolactin (LaHoste, Neveu, Morméde & Le Moal, 1989).

Denenberg and Yutzey (1985) review Denenberg's complex studies on the effects of (preweaning) handling and (postweaning) environmental enrichment upon subsequent behavioural asymmetries in the unilaterally lesioned rat. The RH may be preferentially involved in emotional behaviour and the ability to perform left-right spatial discriminations, and early handling may initiate or augment brain and behavioural asymmetries. Damage to the RH may increase spontaneous activity, though sex and strain differences complicate the picture, while the LH again tends to inhibit emotional reactivity in the RH, probably via the interconnecting corpus callosum. Indeed according to Denenberg, Berrebi and Fitch (in press) male rats pos-

sess wider callosa than females, especially in the genu and the most posterior portion of the splenium, these differences being greatest among those handled in infancy. Sex differences in the thickness of the human corpus callosum have also been reported (Witelson & Kigar, 1988), though the findings are subject to dispute (Byne, Bleier & Houston, 1988).

Glick and Shapiro (1985) review Glick's work with mostly female rats, which were found generally to be more lateralized than males, just as Collins (1985, above) found with mice, and as occurs in humans with respect to motor (but not cognitive) asymmetries. Normal rats tend to turn or rotate, either spontaneously at night or after drug treatment in the daytime, and for any individual the preferred or dominant direction is consistent. Neonatal asymmetries in tail posture may even predict adult turning preferences (cf. the possibility that human head-posture asymmetries in the neonate may predict subsequent hand preferences, Michel, 1981). Unilateral damage to the subcortical nigrostriatal motor system, which contains the neurotransmitter dopamine (DA), causes ipsiversive turning towards the side of the lesion, and this effect can be further potentiated by dopaminergic drugs. In normal rats, too, there are left-right asymmetries in DA concentrations in the two striata, and high doses of d-amphetamine (d-AMPH) increase this DA asymmetry, inducing daytime rotation in the direction contralateral to the side with the higher DA levels. Normal left-right operant preferences also correlate with the direction of d-AMPH induced rotation, and DA levels are normally higher in the striatum contralateral to the rat's side preferences. Moreover rats lacking clear spatial biases may be hyperactive and have learning difficulties in spatial tasks, and may be unable to learn to discriminate left from right (cf. similar claims about dyslexic children, see Bradshaw & Nettleton, 1983); interestingly amphetamine seems to help both children and rats develop a sense of left-right, and, paradoxically, may also reduce childhood hyperactivity (paradoxically, because amphetamine is normally a stimulant). The deoxyglucose (dGlc) technique indicates that the left frontal cortex is normally the more active, and this in turn modulates pre-existing nigrostriatal asymmetries such that measured over a sufficiently large sample, more rats naturally turn right than left. (Indeed Castellano, Diaz-Palarea, Rodriguez and Barroso, 1987, find that in a T maze a majority of rats turn right.) Cocaine inhibits re-uptake of the neurotransmitter dopamine (DA) into the striatum, and enhances rotation, but interacts with sex: after cocaine, naturally right-biased females rotate more than naturally left-biased females, while the reverse occurs for males, though again females are more lateralized, generally, than males. These behavioural sex differences may relate to sex differences in anatomical asymmetries in the cortex and hippo-

campus, whereby the left side is thicker than the right in females and vice versa in males (Diamond, Murphy, Akiyama & Johnson, 1982). Note however that according to Drew, Lyon, Titeler & Glick (1986), asymmetries in the DA receptor densities in the striata, while favoring the right side in females and left in males, are independent of directional preferences exhibited during normal nocturnal circling.

One wonders, though curiously this question seems not to have been addressed until 1987, whether humans might also show natural or drug-induced turning biases. Bracha, Seitz, Otemaa & Glick (1987) measured people's clockwise or anticlockwise turning tendencies, without their awareness, during a routine working day. They found that females have a higher average rate of rotation than males (again indicating that females may be more asymmetric than males in motor behaviour); consistently right-sided males (in terms of hand, foot and eye dominance) showed a rightwards (clockwise) rotational preference, while right-sided females and mixed dominance males showed leftwards (counterclockwise) preferences. On the other hand, Bradshaw and Bradshaw (1988) found that when required to rotate through exactly twice 360° clockwise (rightwards) or counterclockwise (leftwards), blindfolded dextrals, especially females, showed a rightwards bias and sinistrals a leftwards tendency. When however attempting to walk in a straight line all four groups of subjects deviated to the right, especially females and dextrals. Moreover two studies with schizophrenics (Corbin, Williams, & White, 1987, and Reynolds, Czudek, Bzowej, & Seeman, 1987) showed strong clockwise turning tendencies, which both groups of authors believe to be related to increased DA asymmetries, in schizophrenics, in the amygdala or putamen. Further it must not be forgotten that in humans, psychoactive drugs affect emotional and cognitive functioning, which itself is lateralized; so do psychoactive drugs therefore affect lateralized behaviour? Frumkin and Grim (1981) claim that barbiturates, via the action of the inhibitory neurotransmitter GABA, may shift hemispheric lateralization in favour of LH dominance, leading to an increase in loquacity (LH) and a decrease in emotionality (RH).

Before leaving the rodents, we should note (Ehret, 1987) that in the house mouse the ultrasonic calls emitted by the young pups to evoke maternal attention, and which are perceived categorically in the frequency domain, are preferentially recognized by the right ear/LH. Moreover in females without experience of pups, which have been trained to respond to the same signals by conditioning, no asymetries appear. As Ehret observes, mice must have an innate predisposition for attending to and perceiving communication sounds via the LH, even though the mothers must learn to identify them through actual interaction with young. Thus the LH involvement de-

pends upon the *biological significance* of the sounds, just as is the case (see below) with the LH processing of species-specific communicatory sounds by monkeys.

Finally, there are reports of behavioural asymmetries in impala, cats and dogs. There are many more scars on the right sides of male impala, the result of inter-male contests, indicating that the contestants may turn to the left when facing an adversary, which is again compatible with RH mediation of such emotional, agonistic, precopulatory activity (Jarman, 1972). Cole (1955) found that of 60 cats reaching for food in a tube, 20 percent were classifiable as right paw preferring and 38 percent as left; the rest were ambidextrous (defined as less than 75 percent consistent in reaching). Again females were more lateralized. He suggested that a variation in the number of fibres crossing to form the pyramidal tract determines limb preference, but sex differences may be hard to explain thus, and a left paw preference for visually guided reaching is very reminiscent of similar claims (below) with monkeys (MacNeilage, Studdert-Kennedy & Lindblom, 1987). According to Tan & Caliskan (1987a, b), dogs prefer to wipe adhesive tape from the face with their right paws. Moreover while there appeared to be no correlation with paw preferences, Tan and Caliskan (1987a) found asymmetries in the cerebral dimensions and fissures; thus the RH may be longer and higher, but not wider, and the Sylvian fissure on the right side may be lower. Indeed in a later study, Tan and Caliskan (1987b) found that the RH is heavier regardless of paw preference.

MORPHOLOGICAL ASYMMETRIES IN THE PRIMATE BRAIN

Left-right asymmetries in the human peri-Sylvian (speech related) cortex, especially in the region of the temporal planum, have been known for over a century. The Sylvian fissure is generally longer on the left, and continues further horizontally before bending upwards. Its posterior end (the Sylvian point) is usually higher on the right, even as early as the 16th week of gestation, and has been observed in at least two species of fossil humans (LeMay, 1976), *H. sapiens neanderthalensis* and *H. erectus* (Peking Man). The temporal planum, especially the superior portion of the temporal gyrus, an important language area through which the Sylvian fissure passes, is generally larger on the left, even in the fetus; the same holds for another speech area, the parietal operculum (see e.g. Wada, Clarke & Hamm, 1975; Witelson & Pallie, 1973). The left occipital pole is wider and protrudes more posteriorly than the right; anteroparietal and

posteroccipital regions are generally larger on the left. The right frontal pole extends beyond the left, and together with the prefrontal portion of the right hemisphere, is wider (LeMay, 1976; Chui & Damasio, 1980), giving the brain an overall counterclockwise torque. The LH has a higher ratio of grey to white matter (Gur et al., 1980); the right has more tissue and is heavier (LeMay, 1976; Whitaker & Ojemann, 1977).

In the chimpanzee, the Sylvian fissure is also longer on the left (Yeni-Komshian & Benson, 1976), and the Sylvian point is lower on the left in chimpanzees and orangs (LeMay & Geschwind, 1975), due to expansion of the left posterior parietal cortex. Moreover, Falk (1978) studied 88 brain endocasts representing 8 genera of Old World monkeys, and found cortical asymmetries in the lengths of the Sylvian fissure, the superior temporal sulcus, the lateral edge of the orbit and the distance separating the rectus and arcuate sulci. While not all asymmetries matched those found in humans (though in a later study by Falk, Cheverud, Vannier & Conroy, 1986, the length of the left Sylvian fissure of rhesus monkeys was found to be longer, as in chimpanzees and humans), she suggested that a hypothetical expansion of left prefrontal and parietal integration cortices was sufficient to explain these asymmetries, and concluded that the ancestor common to monkeys and humans possessed them. Likewise Sherman, Galaburda, & Geschwind (1982) conclude that during primate evolution the Sylvian fissure has migrated from a nearly vertical to a horizontal posture, due to increasing development of the inferior parietal region which has come, perhaps by a process of preadaptation, to subserve human speech. Again, just as with ourselves, in New and Old World monkeys and baboons the RH frontal and LH occipital regions are wider and protrude further (LeMay, 1985). Indeed Heilbronner and Holloway (1988) report greater Sylvian fissure length in the LH even in *New* World species of monkeys, and de la Coste, Haworth and Woodward (1988) find striate cortex asymmetries even in *lemuridae*, though now it is the right side which is larger, possibly reflecting specializations in visuospatial processing. Finally, Holloway and de la Coste-Lareymondie (1982) studied the petalial asymmetries (projections of the frontal and occipital poles) for 190 hominoid endocasts. They found that all fossil hominids (*Australopithecus*, *H. erectus*, *H. sapiens neanderthalensis*, *H. sapiens sapiens*) showed the same pattern of left occipital and right frontal petalias, while gorilla showed left occipital petalia only. Left occipital width was greatest in all species of *Homo*, *Australopithecus*, possibly gorilla, but not in chimpanzee, leading to the conclusion that 'human' brains are more asymmetrical than those of the pongids, and have been so for 3 million years.

PERCEPTUAL AND MOTOR ASYMMETRIES IN THE NONHUMAN PRIMATE

Horster and Ettlinger (1985) observed that 78 rhesus monkeys spontaneously using the left hand, learnt a tactile discrimination task significantly quicker than 77 spontaneously using the right hand. In humans, the left hand (RH) also tends to be slightly superior at performing tactile discriminations (Bradshaw & Nettleton, 1983). In the visual modality, Jason, Cowey and Weiskrantz (1984) required monkeys to discriminate between squares with a central dot or one displaced slightly upward, before and after a LH or RH occipital lobectomy. In this spatial task for which humans have a RH superiority, animals with a LH lesion (4) all performed worse than those with a RH lesion (5). Likewise Hamilton (1983) found that split brain monkeys learned to discriminate lines differing in slope by 15° much better with the LH. Similarly, Hamilton and Vermeire (1983) tested the ability of each hemisphere of 18 split brain monkeys to learn to discriminate the photographs of faces of other monkeys. Only females (9) showed an asymmetry, a LH advantage, especially animals which were older at surgery. (Perrett, et al., 1988, using single unit recording techniques, claim to have identified the LH regions in the superior temporal sulcus, perhaps responsible for such face processing.) However, later, Hamilton and Vermeire (1985) report a RH superiority as with humans, for face processing by monkeys of both sexes, while confirming their earlier findings of a LH involvement in judgements of line slope. (In a subsequent, 1988, report they confirm and extend these findings of a double dissociation, observing that complementary hemispheric specialization characterized most of their subjects; they also note that, just as with humans, inversion of the facial stimuli eliminates the RH advantage). Ifune, Vermeire and Hamilton (1984) also found that the number of facial expressions elicited from the RHs of split brain monkeys viewing faces was greater than that made by the LH system. For further evidence in chimpanzees of a RH contribution to the perception of (human) faces, chimerically presented (i.e. with left and right halves from differented originals abutted at the midline), see Morris and Hopkins (1989). However we should nevertheless be wary of assuming that asymmetries in other species are necessarily homologous (i.e. of common evolutionary origin) to our own; common evolutionary pressures may bring about similar though otherwise independent (i.e. analogous) patterns of form or function in different species.

It is perhaps in the auditory modality that asymmetries most similar (and perhaps homologous) to our own emerge in the monkey, though as discussed above (Ehret, 1987), a LH specialization for rec-

ognizing pup calls appears in the mouse. Petersen, Beecher, Zoloth, Moody and Stebbins (1978) found evidence of a right ear advantage (REA) in Japanese macaques' abilities to perform discriminations between calls specific to their own species, exactly analogous to our own REA/LH superiority for verbal material. Subsequently Petersen et al, (1984) replicated the above findings, and showed that monkeys of a slightly different species (to whom the taped calls were not species-specific) showed no ear advantage; moreover they demonstrated that both species were attending to the same features, as generalization gradients were highly similar. Heffner and Heffner (1984) trained Japanese macaques to discriminate between two forms of their "coo" vocalization before and after unilateral and bilateral ablation of the temporal cortex. Performance was affected by unilateral ablation of the left (not right) superior temporal gyrus (the analog of our Wernicke's area for speech perception); ablations dorsal to and sparing the auditory cortex had no effect upon discriminations. We must conclude that just as in humans, the temporal cortex of the LH plays a major role in mediating the perception of species-specific vocalizations. Moreover, in an earlier study, we may note that Dewson (1977) trained crab-eating macaques to execute a delayed conditional discrimination between auditory and visual stimuli; lesions in the left superior temporal gyrus again led to more severe performance deficits than damage to the corresponding area of the RH. Finally, Pohl (1983) studied monaural ear advantages for discriminating between members of various acoustic classes in four baboons. Left ear advantages (LEAs) appeared for pure tones in all four subjects, and for three-tone chords in three, for vowel sounds in three, and consonant-vowel sounds (CVs,/pa/vs/ba/) in three. In a subsequent (1984) study he used a gap-detection task requiring resolution of brief silent intervals in noise bursts, and got exactly the same findings as in the previous CV task. Such a RH superiority, in this case indexed by evoked potentials, for humanlike discrimination in a categorical fashion of voice onset time (VOT), was shown by Morse, Molfese, Laughlin, Linnville and Wetzel (1987), working with rhesus monkeys. Humans also evince RH superiorities in discriminating between tokens differing along the voicing dimension, despite the fact that such stimuli are perhaps rather distantly language related.

Turning to motor or response asymmetries, Kuhl (1988) found that all 30 macaques (of 3 species) favored the right hand when making complex, highly-stereotypic manipulative responses, despite often using the other hand in simpler situations. Preilowski, Reger and Engele (1986) required rhesus monkeys to produce specific pressures for specific times with the fingertips; while individuals showed extreme degrees of hand preference which were nevertheless independent of hand performance, when difficulty levels were adjusted to the perfor-

mance of each hand, the *right* (but not necessarily the *preferred*) hand proved superior. Indeed Falk, Pyne, Helmkamp and DeRousseau (1988) report that out of 150 rhesus monkeys, 7 out of 10 forelimb dimensions are larger on the right, especially those relating to the ulna and humerus. The authors speculate that such hypertrophy reflects greater use, as similar relationships are found in humans. In the baboon, Vauclair and Fagot (1987) report that of a troop of 18, 5 showed a right hand preference for spontaneous activities and 2 a left hand preference—hardly a major asymmetry when 11 were ambilateral—though a developmental increase was apparent. However in a companion paper (Fagot & Vauclair, 1988a) they found a *left* hand preference in the baboon for complex novel manipulations requiring fine visuospatial discrimination—an issue to which we shall return shortly. In the lowland gorilla these authors (Fagot & Vauclair, 1988b) also obtained a left-hand preference (7 out of 8 animals) in a precise manipulospatial task similar to that employed above with the baboons, while hand differences were absent when the animals simply reached for objects. (They also reviewed a number of earlier minor and largely observational studies employing between one and 8 animals: out of 18 gorillas, 15 were reported as preferring the right hand and 1 the left in relatively stereotyped situations.) A possible resolution of these conflicting data is indicated by the findings of Sanford, Guin and Ward (1984). They studied 25 bushbabies for hand preferences for reaching for and grasping objects; only under conditions of an obligatory bipedal stance did a left hand preference emerge. (Ward, 1988, later noted that a left hand bias in food reaching is a salient characteristic that extends across several species in prosimians). These findings were taken up by MacNeilage, et al. (1987) in their review and re-analysis of old data. They argue for a *left* hand superiority for visually guided reaching, and a *right* hand preference for manipulation and practiced performance in stereotyped situations, though they have been criticized for inappropriate statistics and for ignoring many null findings. They claim that earlier negative conclusions arose from use of juvenile animals, or tasks which did not adequately call upon such preferences. They suggest that primate handedness patterns are structural, and a functional adaption to feeding, and are precursors to aspects of human LH and RH specializations. Specifically, they suggest that a left-hand RH specialization for visually guided reaching occurred in early prosimians, which were vertical clingers and leapers. This led to two complementary specializations, a left-hand, RH perceptuomotor specialization for unimanual predation, perhaps with visuospatial components, and a LH (right-limb) specialization for whole-body postural organization, again perhaps associated with a pre-existing LH mediation of communication. With the advent of quadrupedalism, from a vertical leaping and cling-

ing posture, the right forelimb undertook manipulation, and now the left side of the body reversed roles to undertake postural support. Consequently, they emphasize the important predictive role of footedness in humans, claiming that a right foot dominance is more strongly linked with language lateralization than is handedness (MacNeilage et al., 1988), though see Peters (1988) for problems in dissociating the postural and the active aspects of foot asymmetry. Such an account, however, only accommodates with some difficulty the findings of asymmetries among birds and rats, and there is much evidence that speech and other cognitive specializations in the LH precede manual asymmetries, both phylogenetically and ontogenetically. Thus far more of us have some left hand preferences (the writing hand not always being the preferred hand for all other tasks) than have RH language, manual skills being more flexible with respect to hemispheric specialization than language skills, as evidenced both by the clinical and the learning literature. Moreover, as Michel and Harkins (1987) observe, it seems maladaptive for humans to have now lost a left-hand bias in reaching (the LH/right hand system presumably having taken over *both* functions) as an object would have to be transferred from right to left hand if it is to be bimanually manipulated or worked on by the right hand. Michel and Harkins also note that during infancy a right hand bias for reaching *precedes* the appearance of bimanual manipulation. When the latter appears, infants often switch reaching preference to the formerly nonpreferred hand, to facilitate using the preferred hand for more active manipulation, and only later revert to using the right hand for both reaching and manipulation, necessitating a fumbling intermanual transfer. For these reasons, bimanual manipulation seems to be an unlikely source of a right-hand bias in reaching. Our use of the right hand both for reaching and manipulation may reflect the emphasis in our manual behaviors of rapid, accurate, sequential activities of a temporal rather than a purely spatial (RH) nature; thus the precise temporal integration of a number of sequential movements (as in reaching, grasping and then manipulating an object) may outweigh the purely spatial components, which could nevertheless continue to feed, albeit indirectly via ipsilateral pathways, to the right limb. Indeed under certain conditions emphasizing the more spatial aspects of reaching, a left-hand superiority and/or a RH contribution may appear (for review, see Goodale, in press).

HOMINID ORIGINS AND POSSIBLE EARLY DEXTRALITY

There is substantial current disagreement concerning the details and chronology of hominid lineage (Andrews, 1986; Lovejoy, 1981;

Stringer & Andrews, 1988). Hominids and African apes probably split between 9 and 5 million years ago, due perhaps to major environmental changes, though the hominid-chimpanzee split would be closer to the lower figure. Indeed in terms of genetics (DNA sequencing and hybridization techniques) and evolutionary time, we are probably closer to chimpanzees than the latter are to gorillas (Lowenstein & Zihlman, 1988), despite the fact that chimpanzees and gorillas look more alike; both are hairy, walk on all fours, knuckle walk, have short legs and long arms, brachiate, are less dextrous manually than ourselves, have smaller brains and larger canine teeth with thin enamel. Thus apparent chimpanzee-gorilla similarities do not necessarily reflect closeness of kinship, or convergent evolution, so much perhaps as retention of ancestral traits which we have lost. Our own physical differences from chimpanzees, despite the close genetic similarity, probably stem from the fact that much of our joint genetic make-up is in fact largely nonfunctional in both species without an impact upon morphology, thus even permitting it to be used as a clock for genetic change or drift uninfluenced by selective pressures.

By 4 million years ago, species of the hominid *Australopithecus* had emerged. Our possible ancestor *A. afarensis* may have produced the dramatic and seemingly-fully-bipedal footprints preserved at Laetoli 3.5 million years ago (Leakey & Hay, 1979): even if posture was not fully modern (though see Lovejoy, 1988), bipedalism seems to have greatly antedated brain enlargement and the emergence of tools. The African hominids split into the gracile (*A. africanus*) and robust (*A. boesei*) australopithecines, and our first probable ancestor *H. habilis*, before 2 million years ago; the human fossil record is limited to Africa for the first 3 million years. (It is possible that more than one species may currently be "lumped" into *H. habilis*, and certain that this—or these—species co-existed with other australopithecines.) The first undisputed stone cultural remains (*H. habilis*, Oldowan culture) appear 2.5 to 2 million years ago. Indeed, according to Toth (1985), *H. habilis* was habitually dextral, to judge from an analysis of the pattern of successive flaking from stone cores: thus dextrals typically hold the core in the more passive left hand and rotate it clockwise. The resulting sequence leaves its trace of superimposed scars on the flakes; these Toth believes were used as tools, rather than the residual cores. Whether or not these conclusions are upheld, it is interesting to note that there is quite separate evidence in that species (Bahn, 1989) from the presence of characteristic grooves, together with reactive ridges, along the junction between cementum and enamel, of the use of toothpicks at Omo (Ethiopia) by 1.84 million years ago. These patterns, not otherwise accountable for by e.g. root caries, gritty saliva or fibre processing, are similarly found in all later species including ourselves, and are indicative of prolonged re-

petitive action. Yellen (1986) observes that *H. habilis* was the first hominid with an enlarged cranium (600 to 800 cm^3).

The transition from *H. habilis* to *H. erectus* (Java, Peking Man, the Acheulian stone tool culture) probably occurred at about 1.5 to 2 million years ago; the latter had a still larger brain (800 to 1200 cm^3) and more advanced tools (bifacials) and possibly fire. (Brain & Sillen, 1988, report burnt bones heated to a range consistent with campfires in the Swartkrans cave Member 3 layers, dated to between 1.0 and 1.5 million years ago; only the remains of *A. robustus* were found associated, though *H. erectus* was presumably also present. Thus there is the possibility even of australopithecine use of fire.) *H. erectus* at 1.5 million years ago constructed flint axes *around*, and thereby preserving spectacular fossils in a prominent central locus, perhaps to serve as a "personal blazon" (Oakley, 1981). (It could be argued that the concretionary nature of the flint nodules around fossil nuclei was such as to inhibit flaking in the immediate vicinity of the core fossil, thereby artifactually leaving the fossil in a prominent central position). Shortly after, the australopithecines which had hitherto coexisted with *Homo* became extinct (1.3 to 1 million years ago). De Castro, Bromage, and Jalvo (1988) analyzed the orientation and location of striations on the anterior teeth of anteneanderthal hominids from the Spanish Middle and early Upper Pleistocene. They concluded that the patterns were indicative of antemortem stone tool use to cut meat held between the teeth, preferentially by the right hand (and see also Bromage & Boyde, 1984). While archaic *H. sapiens* at 0.5 million years ago was African (Andrews, 1986), and the same was perhaps true of modern *H. sapiens* (which much later developed the European Cro-Magnon culture) at about 100,000 years ago, nevertheless the latter date has now been proposed for its arrival in the Levant (Valladas et al. 1988). Neanderthals (with their Mousterian stone tool culture) were probably not closely related phylogenetically, and may have subsequently arrived there at a relatively late date from Europe, where they might have emerged 300,000 years ago. They became extinct around 35,000 years ago, perhaps in competition with modern *H. sapiens*.

BIPEDALISM, TOOL USE AND THE ORIGINS OF LANGUAGE

While the use of language, tools and an upright bipedal posture and locomotion are characteristics not totally unique to humans, all three only appear consistently in our own species. Thus, depending upon the definition of language, and resolution of arguments concerning whether or not apes taught (painfully) to communicate with us are capable of deliberate deception and formulation of totally novel

sequences etc. (Premack, 1986), apes may or may not be said to employ language. Moreover other species may occasionally move bipedally, and use tools (Beck, 1980), and maybe even partake of some form of consciousness (Griffin, 1984). Whatever may be the case with *A. afarensis*, *H. habilis* undoubtedly possessed an upright bipedal posture, though debate continues whether this posture was acquired early (Lovejoy, 1988), or gradually (Jungers, 1988), within the latter instance individuals dividing their time between trees and ground. Thus Lovejoy (1988) argues that the 3,000,000 year old australopithecine female "Lucy" was even *better* designed for bipedalism than we are, to judge from the shape of her pelvic ilium and femoral neck; this was so only because the resultant constriction (relative to that of a modern woman) in her birth canal was tolerable because her species predated the dramatic expansion (see below) in fetal head size at birth. Lovejoy goes on to claim that her bipedal progression was truly habitual, all other kinds of locomotion having been foresaken, as the particular muscular rearrangements enabling her to walk upright would not have permitted efficient quadrupedal locomotion on the ground. He does at one point allow that she might often have taken to the trees and climbed, as most primates do, using all four limbs. Later, however, in the same article, he appears to explicitly disallow even this possibility. Indeed, according to Latimer and Lovejoy (1989), the calcaneus in the foot of *A. afarensis* had already undergone the primary adaptive alterations to bipedality seen in *H. sapiens*, indicating that a completely terrestrial life-style was responsible; these authors conclude that it is highly unlikely that significant climbing behaviours were included in the locomotor repertoire of that species. On the other hand, according to Jungers (1988), compared to ourselves, apes have curved hand and foot bones, small hindlimbs and a rather different lumbo-sacral structure, with *fully* modern morphology in every respect possibly not appearing until *H. erectus*, which might have been the first to habitually employ a true striding gait. (Susman and Brain, 1988, report finding a hallucal metatarsal bone from the Swartkrans cave, dated to ca. 1.8 million years ago, and attributed to *Paranthropus (= Australopithecus) robustus*; closely resembling that of humans, it suggests a human like posture and range of foot movements, though the human "toe-off" in walking may have been absent. Thus *H. habilis* and surviving austalopithecines may have attained a similar grade of bipedality at that date.) While *H. habilis* may therefore have possibly retained a mosaic of primitive and derived features (and see Susman & Stern, 1982), it could nevertheless also fabricate simple cobble tools, the first undisputed stone tools in the archaeological record. Whether or not climatic changes occasioned its ancestors' move to the open savannah (other lineages of course successfully remained in a forest environ-

ment), its upright posture may have been pre-adapted for by retained habits of brachiation while seeking opportunistic or nocturnal arboreal refuge: similar musculature to upright walking is employed in tree climbing.

Hardy (1960, and see also Morgan, 1984, 1986) instead proposed an aquatic phase in hominid evolution, leading to loss of body hair, the presence of subcutaneous fat, face to face copulation (as in all aquatic animals), the presence and distribution of fetal hair, weeping (salt excretion), the diving reflex (apnea, bradycardia) and of course bipedalism, as swimming is said again to employ similar musculature. However there is no paleoclimatic evidence for the proposed widespread flooding; moreover other explanations can account for our nude skin, e.g. the dissipation of excess metabolic heat during temporary exertion, such as fleeing predators, or opportunistically pursuing small savannah prey. Indeed a new ecological niche would be opened for hominids were they to do the latter during noonday heat. Furthermore, bipedalism is itself a thermoregulatory advance, removing much of the body from close proximity to the heated ground, and exposing less skin to the sun's rays. Such a thermoregulatory advance (Ebling, 1985; Wheeler, 1984), together with a massive increase in sweat glands (themselves of course useless in water) would remove a barrier to further brain growth. A large brain is itself also a considerable source of metabolic heat. However, even these factors on their own may have been insufficient to account for the adoption of a posture which is so unfavorable for speed and agility.

Other factors which favor bipedalism and ultimately dextrality include missile throwing (Calvin, 1983) and tool use (Frost, 1980). The latter factor really subsumes the former. Thus manual specialization would result in one hand holding a store of missiles, and the other throwing, or one hand holding and steadying an object, while the other hand sequentially operates upon it, with consequent economies of brain processing space. Indeed Frost emphasises the sequential syntactic character of both tool operations and language, and suggests that this may be why both functions are co-lateralized to closely adjacent regions of the LH. These peri-Sylvian regions seem from electrostimulation studies (Ojemann, 1983) to be essentially motor, whether for sequencing, temporal ordering or precise perceptual timing. Such *perceptual* aspects, as in discrimination between heard phonemes during speech perception, suggest that speech perception itself may depend upon the mechanisms otherwise used for speech *production* (Liberman, Cooper, Shankweiler & Studdert-Kennedy, 1967), and that there are close anatomical and functional links between manual and oral movement control, speech production and perception (and see Kimura & Harshman, 1984). Such considerations, however, do not necessarily imply that gesture must have preceded language

(see below), or that tool making or tool using behaviors *presuppose* some form of syntactic language (Holloway, 1981), since even the simplest of such behaviors are notoriously difficult to describe and are far more easily transmitted by example or imitation. Imitative learning in fact is an additional factor which we can invoke to account for asymmetries at the *population* level, the fact that most individuals in a population are lateralized in the same direction. Thus two dextrals (or two sinistrals, i.e. two individuals of the *same* handedness) learn more efficiently from each other how to tie knots (Michel & Harkins, 1985), a possible paradigm of tool use acquisition. However as discussed above, *H. habilis* may already have been dextral, and anyway tools, until maybe *H. erectus*, were hardly of the complexity that interactive or imitative learning would benefit from homogeneity of handedness. (Indeed the techniques available to *H. habilis* of essentially clumsy rock-bashing probably only permitted a limited range of possible artifact shapes, thus obviating the need for either language or careful imitation.) We must therefore conclude that dextrality appeared either much earlier, for other reasons, or much later. In any case while evolutionary pressures may have favored either uniformity of handedness, for whatever reasons, or outright dextrality (which of course is not *itself* presupposed by uniformity of handedness), we should note that there may be certain residual advantages in sinistrality; such individuals can often use their nonpreferred hands more efficiently than dextrals (Kilshaw & Annett, 1983), and may under certain circumstances even be superior in spatial skills (Benbow, 1988; Geschwind & Galaburda, 1985).

Parker and Gibson (1979) propose their own version of the tool use hypothesis in the context of a general theory of the evolution of language and intelligent behavior. They suggest that expanded tool use developed as an aid for extractive foraging. The latter, rather than hunting, differentiated hominids from the apes, and involved hammering, digging, stabbing, probing, hitting, cutting and ultimately throwing; it led to food sharing and on to language, via gesture. However, their particular argument relies heavily upon ontogeny recapitulating phylogeny, at the levels both of brain and of behaviour, and upon Piagetian stages of intellectual development in children and other species, two areas currently of some controversy. Nevertheless, the general scenario of an upright posture leading to tool use, gesture and on to language (Hewes, 1976) is a popular one: we readily fall back upon gesture; retardates may rely upon it, and we can teach chimpanzees a gestural channel of communication with us; among primates only humans possess unpigmented (i.e. clearly visible) palms; gesture is superior to speech in showing how to do things; there may be syntactic commonalities between gesture, tool use and butchery; gestures precede or are synchronous with speech;

an intervening gestural stage would separate the supposedly involuntary subcortical calls of other primates from the voluntary, cortical and propositional language of humans. As we shall see, this last distinction may well be invalid, and in any case there is a major problem with the late location of gesture in the sequence. Thus chimpanzees (and therefore presumably a common ancestor of chimpanzees and of our own species) share many of our gestures (Harré & Reynolds, 1984), despite not being habitual tool users. Indeed increasing tool use might well have *hampered* gesture and instead favoured a vocal/auditory channel of communication, as also would have the need to communicate at a distance, in the dark or among vegetation (Hewes, 1973, 1977), though problems associated with vocal rather than gestural communication include, e.g., interference with breathing and swallowing, and arousal of predators and prey. Moreover, the fact that chimpanzees can be taught to sign, but not to speak, with cognitive powers probably similar to those of the early hominids, does not prove the priority of gesture over vocal language, whether or not we can decode "gesturelike" written characters faster than speech. Thus some would argue (e.g., Count, 1974) that human infants learn vocal speech *before* gesture.

A general problem with the tool-use scenario is that it seems to have progressed and developed extremely slowly; it first appeared 2.5 to 2 million years ago, a standard "tool kit" emerging 1.5 million years ago, with no other major advances until 300,000 years ago, despite enormous increases in brain size (Calvin, 1987). Toolmaking would not therefore seem to be a major evolutionary force behind increases in brain size, or other evolving behaviours, e.g., language. Indeed Susman (1988) reports that small-brained *A. robustus* (a descendent of earlier australopithecines) at 1.8 million years ago possessed a hand adapted for precision grasping and may have used tools (though tools associated with the remains could instead have come from *H. erectus*). While he concludes that tool acquisition might not therefore account for the emergence and success of early *Homo*, and the absence of tool behavior would not have been responsible for the (competitive) demise of *A. robustus*, it should be noted that the tool kit of the putative competitor, *H. erectus*, was considerably more advanced than any others present or before.

It is possible that several factors (e.g. food carrying, family bonding and an altricial juvenile phase) co-evolved in a mutually synergistic or facilitatory way, rather than occurring, as traditionally conceived, in a linear sequence. While it is certainly easy to invoke complex interactions between a number of factors, medical pathology often requires the interactive co-occurrence of several (not always the same) factors from among a larger subset. Multifactorial interactions are also evident in ecological equilibria. Language (and specialized

modes of cognition, thought and conscious awareness, cf. Jaynes 1977) may be seen as developing as an inevitable concomitant of increasing cortical development. The latter was perhaps demanded by survival needs in the new ecological niche created by climatic deterioration. This would have required a change in habits of acquiring and sharing food, e.g., socially cooperative foraging, hunting and butchering (see e.g. Isaac, 1983; Parker & Gibson, 1979). In addition to the other advantages conveyed by bipedalism (thermoregulation, improved vision, hands free for carrying and using tools and weapons) and in addition to its possible arboreal origins thereby favoring gripping, releasing, pulling, poking, picking, waving, hitting, throwing etc. (Richards, 1987), it would have been an essential adaptation for cooperative foraging. While a substantial increase in brain size (which cannot simply be explained as an allometric effect of a concomitant but much smaller increase in body weight) and the use of tools both undoubtedly long postdated bipedalism, nevertheless with an increase in the size of fetal heads, mothers had as it were to compromise between a walking pelvis and one which could accommodate the fetus at birth. A solution (and see Lovejoy, 1981) was perhaps a prolonged postnatal development, with a shift to learning, socialization, parenting, family bonding, a home base controlled by the mother, and foraging activity. The latter could have been accomplished by the father, perhaps more as a scavenger than as a hunter, and of meat rather than of vegetable products, to transport and furnish sufficient protein for a family of three, and to provide the structural fats required for the development of a large brain (Crawford & Sinclair, 1971, cited in Ebling, 1985). While early hominid teeth seem in terms of morphology and wear patterns to be characteristic more of plant than of meat eaters (Lewin, 1987), and modern hunter-gatherers may rely more upon the vegetable products of female foraging than the animal products of male hunting, the opportunistic carnivory of the predominantly vegetarian chimpanzee might provide an appropriate model. The multifactorial-interactive account (Holloway, 1981; Wind, 1983; see also Commentary to Parker & Gibson, 1979, especially Gould, Gruber, Isaac, Jolly and Lamendella), therefore invokes an enlarging neocortex, bipedalism, a characteristic dentition (reduced anterior, with molar dominance), an increasingly material culture, and unique social (Byrne & Whiten, 1988), sexual and reproductive behavior (Lovejoy, 1981), rather than the evolution of intelligence simply to solve ecological problems or to manufacture and use tools. Thus intense social pressure (the need to deal adequately with fellow group members, to obtain and provide social favors, to participate in alliances, to deceive and to dominate) and the needs of parenting (which are still evident today) would provide the evolutionary driving force for an enlarging brain and, ultimately, tool use, a mate-

rial culture, and advanced communicatory skills. With the development of language, genetically programmed behavior could now be subordinated to learnt cultural programs. The recurring suggestions of a division of labor between the sexes (spatially-oriented hunting and foraging by the male parent, the development of the offsprings' social and communicatory skills by the female) are reminiscent of two claims; on the one side that males may be slightly superior to females with respect to spatial abilities and correspondingly inferior verbally (Halpern, 1986; McGlone, 1986), and on the other that in females there is a more focal and anterior representation of speech and manual praxis (Kimura & Harshman, 1984). Kimura (1983) speculates that this situation might improve the precision and speed of fine motor skills and speech control, important aspects for a home-based parent, while the father would have benefited from a more diffusely represented posterior (i.e. *perceptual*) mediation of spatial skills for foraging and hunting, where fine manual dexterity and fluent speech is less important.

Despite the comparatively primitive nature of the tools of *H. habilis*, and the fact that upright walking and tool use might have been possessed by contemporaneous australopithecines (see above), new studies of brain endocasts of Olduvai specimens of *H. habilis* (Tobias, 1987) indicate that that species was closer to *H. erectus* than to the australopithecines. Thus *H. habilis* possessed a disproportionate expansion of frontal and parieto-occipital regions, especially in the two areas governing speech in modern humans, so much so that Tobias concludes that it possessed the structural markers of the neurological basis of spoken language.

Jerison (1982) also believes that language evolved in response to an environmental demand for additional cognitive capacity, rather than specifically for new and better communicatory skills. As he observes, had its evolution been driven solely by the need to communicate the sorts of things that *other* predator and prey species are vitally interested in, the resultant system would probably have been far simpler, less flexible, less ambiguous, and less demanding of processing capacity. However, his conclusion (shared with Chomsky, 1980, see below), that human language could not at the same time have evolved from earlier primate call systems, may be less secure.

IS LANGUAGE "SPECIAL" OR CONTINUOUS WITH PRIMATE VOCALIZATIONS?

According to Chomsky's nativist account, our language ability derives from an innate language-specific neural mechanism, with no prior evolutionary history, no prior preadapting counterparts in ear-

lier species, and no biological precedent. (Compared to this "creationist" viewpoint, more extreme even than one which could be accommodated in terms of a punctate evolutionary process, the corollary idea, that there is a common deep structure to all languages and grammars which is independent of meaning, is less controversial.) However, there is abundant evidence for the evolutionary utilization and adaptation of pre-existing structures for new functions; the swim bladders of lung fish became lungs, the airway between lungs and mouth was adapted for phonation, and many other peripheral and central structures have been adapted in our species for speech, the most complex motor activity of which mammals are capable. Thus Lieberman (1985) agrees with Chomsky only to the extent that the sounds of speech are special, permitting data transmission 10 times faster than what is attainable by any other signals in the auditory domain. Like other complex yet automatic human and primate motor skills, it involves rapid goal-directed responses *towards* target loci, in the absence of innate control mechanisms to cope with every possible starting point. It involves reflex-like motor control mechanisms which can compensate (within 40 msec) for any unexpected imposed environmental perturbation. Nevertheless nonhuman primates seem to have neither the oral nor the neural capabilities of producing the full range of human speech sounds that are acoustically distinct and resistant to articulatory perturbation. The descent during evolution of the supralaryngeal tract, perhaps partly as a consequence of the adoption of an upright posture, and an adaptation permitting the development of a wide range of articulatory gestures, has however been at the expense of efficient respiration, swallowing and chewing. In addition, the tongue has been recessed, and the jaw shortened with a reduction in the number of teeth, adaptations which facilitate speech at the expense of eating. Other species (including the human neonate, thereby disproving claims of human neoteny) can breathe while drinking; they do not choke since the epiglottis can connect the larynx directly to the nasal cavity, sealing it off while swallowing. (Wind, personal communication, 1989, March 8, nevertheless observes that with a population of 5 billion our throats must nevertheless function reasonably efficiently.) Lieberman believes that neanderthals lacked the supralaryngeal tract characteristic of modern adult *H. sapiens sapiens*, based on his soft-tissue reconstruction from fossil skull-base anatomy; the neanderthals would therefore have lacked the requisite articulatory control mechanisms, and would have been capable of greatly reduced communicative abilities. However, Wind (1978) queries the accuracy of the vocal tract reconstructions, and observes that even if they are accurate they may not be relevant for assessing ancestral speech capacities, given the enormous redundancy of the human tract (as evident from pathology, e.g. intelligible speech being

possible even with partial laryngectomy). Indeed other species (e.g. parrots) can give very passable imitations of human speech. Thus if a modern human possessed Lieberman's reconstruction of a neanderthal vocal tract, his speech might be only slightly depauperate. In fact the discovery (Arensburg et al., 1989) of a well-preserved neanderthal hyoid bone, dating from about 60,000 years ago, which is almost identical to those of present day populations, suggests that there has been little or no change to laryngeal structures, and that neanderthals possessed the morphological basis for modern speech capability.

What can we say about the possible evolution of the *neural* mechanisms to drive our articulatory, phonological and syntactic capacities? Lieberman again rejects the Chomskian viewpoint, in favor of an evolutionary continuum from neural mechanisms which facilitated complex, skilled automatized motor behavior in earlier species during the previous 0.25 million years. He believes that speech evolved in two stages: what is now Broca's motor speech area initially came to control *noncommunicative* aspects of the orofacial musculature, and later was modified for the automatization of the complex articulatory manoeuvres necessary to produce rapid encoded speech and rule-governed phonology and syntax. He appeals to preadaptation acting upon the neural substrate governing complex orofacial movements in these earlier primates, and argues that our species-specific speech areas in the brain, required both to produce an acoustically complex signal and to unscramble what is heard, evolved in synchrony with the human supralaryngeal tract. Of course it could be argued (cf. Count, 1974, and Wind, 1978) that our information processing capacity evolved *before* a modern vocal-tract morphology, as our symbol decoding capacity, as in reading, is far faster than the speeds achievable with articulatory speech.

Could the evolution of human speech therefore have been built upon and been continuous with earlier primate vocalizations and vocal-auditory signalling? Traditionally (see e.g., Malmi, 1976) monkey calls convey information only on the signaller's location and motivational state, being involuntary, nonpropositional, nonreferential, nonsymbolic, and controlled by subcortical centres of limbic affect. Thus Dingwall (1988) reviews evidence that the control of nonhuman primate *vocalization* (as distinct from *reception*) terminates at the supplementary motor area, which in humans is thought to mediate the planning of complex volitional motor sequences. While ablation in monkeys of homologs of human language areas has little appreciable effect upon vocalization, the same may not of course be true with respect to reception. Our speech, on the other hand, consists of voluntary propositional communication, which involves cortical mediation and learning. However monkey vocalization both in the wild and in

the laboratory has recently been found to be far richer and more flexible than previously thought (see e.g. Steklis, 1985), conveying information on sex, personal identity, group membership, social relationships and at least three different kinds of predator; thus a particular alarm call will evoke the appropriate kind of looking behaviour in listeners. Indeed, while our *own* speech *also* depends heavily upon subcortical (thalamic, basal ganglia) mechanisms (Crosson, 1985), as we saw earlier (Heffner & Heffner, 1984) monkeys may employ cortical areas in the LH homologous to our own speech centers, at least at the level of reception. This all suggests a direct continuum from the common ancestor of monkey and humans (maybe even down to the level of the rodents, see Ehret, 1987, above) for a LH mediation of auditory communication.

Falk (1980, 1987) also believes that our vocal language has a long evolutionary history, continuous with an early primate call system in an arboreal habitat; that *some* form of language was selected for *before* bipedalism, tool use and gesture; and that developed tool use presupposes language. (Jaynes, 1977, disagrees; as he observes, even our *modern* language can no more describe how to make or use a tool than it can instruct one how to learn to ride a bicycle). While language may not have been useful in instruction in this respect, it could be argued (again cf. Jaynes, 1977) that language potentiated the cognitive strategies for successful tool manufacture and use. Again, it may be objected that, until perhaps 50,000 years ago, tool deployment was at a comparatively simple level. Holloway (1976) believes that the australopithecine brain was large enough to accommodate some form of language; certainly modern microcephalics with a brain ($300cm^3$) in the chimpanzee range, though severely retarded, possess some speech and reasonable sensorimotor abilities (Jensen-Jazbutis, 1970, cited in Jerison, 1982). Why then do chimpanzees not learn to speak? They can of course be taught to communicate after a fashion, but dogs can be taught to walk on their hind legs for short distances without showing any natural innate predisposition to be bipedal. On the other hand Man may acquire some degree of language even against enormous odds (e.g. deafness or partial isolation). Some form of communication *can* be taught to the great apes. However debate continues (Premack, 1986) about the true status of chimpanzee and gorilla nonverbal language capacities (e.g. is it true language, can and do chimpanzees prevaricate, can they invent new strings in new and appropriate syntactic order, is it just a "clever Hans" phenomenon, is it smart problem-solving but nonlinguistic behaviour, how should we *define* language . . . ?). While we should perhaps reject the Chomskian view of the absolute uniqueness of language to *H. sapiens*, nevertheless certain conclusions (see Lenneberg, 1967) should be born in mind: we do have anatomical specializations (neu-

rally, and peripherally) for language, even though they may be directly evolved from nonhuman primate structures; critical periods for language acquisition in the developing child are universal in all races everywhere; language cannot easily be suppressed by isolation, even though it cannot be acquired if the individual is isolated beyond certain critical periods (Fromkin, Krashen, Curtiss, Rigler, & Rigler, 1974); it can only be taught, in highly modified form, with great difficulty or not at all to other species; linguistic universals appear to exist; certain language dysfunctions are heritable; all cultures possess language; the laboured artificial process of learning a second language in adulthood is quite different from the ready natural acquisition of the first language; even neonates exhibit language lateralization, and move in synchrony to the rhythms of speech (see e.g. Leahey & Harris, 1985, Ch. 11). While therefore language may not be totally unique to our species, and may have evolved from earlier forms of communication, in its present form it is very substantially different to anything which might have preceded it.

The viewpoint most directly opposed to the one that language has a long evolutionary history argues that around 50,000 years ago an innovation occurred in how we communicate (Davidson & Noble, 1989; Jaynes, 1977; McHenry, 1982). At that time artifacts and art dramatically increased in complexity. Jaynes believes that this reflects the sudden appearance of language. This eventually permitted humans to achieve (self)consciousness, the latter (and language in its "modern" guise) not emerging until literally the last few thousand years, according to Jaynes, in the vicinity of the Mediterranean and the Near East. (Such a late date ignores the much longer independence and isolation of e.g. the Australian aborigines.) In any case as Jerison (1982) observes, and comparative psychologists are increasingly assuming (see e.g. Griffin, 1984), some form of consciousness is probably not restricted even to the primates; the same of course is true of tool use (Beck, 1980), where one detached object separate from the user's anatomy is used to change the state of another. This is not to deny that a great change occurred in the archaeological record after 50,000 years ago, and even glottochronological studies based on the rates of "modern" language change converge upon a figure of around 40,000 years for a putative ancestor of most extant tongues (Miller, 1981; Ruhlen, 1987). However this change could simply reflect the reaching of a "critical state" in technology, society and communication, a flowering of potentialities and precursors with a long evolutionary history, rather than a wholly new innovation. It is interesting to note that in a detailed analysis of modern gene distributions to reconstruct the phylogeny of extant human populations, Cavalli-Sforza, Piazza, Menozzi and Mountain (1988) recognize six main pop-

ulation clusters, the oldest split being between African and the remaining clusters, which then progressively fractionated further. For each of Ruhlen's (1987) 17 language phyla, aboriginal speakers of all the languages in that phylum belonged to the same genetic cluster proposed by Cavalli-Sforza et al. (1988). Thus at long last there arises the possibility of bringing together genetic, archaeological and linguistic data, as Cavalli-Sforza et al., observe in the very title of their article.

CONCLUSIONS

There may be a continuity with earlier species of our two most obvious asymmetries, language lateralization, and movement control and sequencing by either hand. Indeed there may be an ancestral LH specialization for sensory and motor discrimination learning. Perhaps by default (Corballis & Morgan, 1978) more primitive spatial and emotional functions were relegated to the RH, though we cannot exclude the possibility that the latter hemispheric specializations instead were in fact the prior ones. However in all species, asymmetries tend to be quantitative rather than all-or-nothing, and subject to effects from sex and development. The (disputed) left-hand preference in primates for visually guided reaching may reflect the contribution from the RH of (visuo)spatial control, rather than simply being a consequence of the right hand pre-empting a postural role. Inhibitory control processes involving higher learning in the LH might have subsumed the development of communicatory processes, together with practised manual responses; hence the close cortical proximity of our centers for speech and manipulation. Our two basic LH functions, communication and manipulation, are however only loosely linked to each other, each being independently associated with that hemisphere's original specialization for higher sensory and motor discrimination learning; hence dextrality, and LH mediation of communication and manipulation, often dissociate. Finally, if modern language first appeared around 50,000 years ago, it was probably not a sudden evolutionary innovation so much as the attainment then of some kind of "critical mass" in the make-up of society.

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REFERENCES

Adret, P., & Rogers, L.J. (1989). Sex differences in the visual projections of young chicks: A quantitative study of the thalamofugal pathway. *Brain Research, 478*, 59-73.

Andrew, R. J. (1983). Lateralization of emotional and cognitive function in higher vertebrates, with special reference to the domestic chick. In J. R. Ewert & D. Ingle (Eds.), *Advances in vertebrate neuroethology* (pp. 477-510) New York: Plenum.

Andrew, R.J. (1988). The development of visual lateralization in the domestic chick. *Behavioral Brain Research, 29*, 201-209.

Andrew, R. J., & Brennan, A. (1985). Sharply timed and lateralized events at time of establishment of long term memory. *Physiology and Behavior, 34*, 547-556.

Andrew, R. J., Mench, J., & Rainey, C. (1982). Right-left asymmetry of response to visual stimuli in the domestic chick. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 197-209) Cambridge, MA: MIT Press.

Andrews, P. (1986). Fossil evidence on human origins and dispersal. *Cold Spring Harbor Symposia on Quantitative Biology, 51*, 419-428.

Arensburg, B., Tillier, A.M., Vandermeersch, B., Dudey, H., Schepartz, L.A. & Rak, Y. (1989). A Middle Paleolithic human hyoid bone. *Nature, 338*, 758-760.

Babcock, L.E. & Robinson, R.A. (1989). Preferences of Paleozoic predators. *Nature, 337*, 695-696.

Bahn, P.G. (1989). Early teething troubles. *Nature, 337*, 693.

Beck, B. B. (1980). *Animal tool behavior*. New York: Gordon.

Benbow, C. B. (1988). Sex differences in mathematical reasoning ability in intellectually talented pre-adolescents: Their nature, effects and possible causes. *The Behavioral and Brain Sciences, 11*, 169-232.

Bianki, V. L. (1983). Hemisphere lateralisation of inductive and deductive processes. *International Journal of Neuroscience, 20*, 59-74.

Borod, J. C. & Koff, E. (1984). Asymmetries in affective facial expression: Behavior and anatomy. In N. A. Fox & R. J. Davidson (Eds.) *The psychobiology of affective development*. (pp. 293-323). Hillsdale, NJ: Erlbaum.

Bracha, H. S., Seitz, D. J., Otemaa, J., & Glick, S. D. (1987). Rotational movement (circling) in normal humans: Sex difference and relationship to hand, foot and eye preference. *Brain Research, 411*, 231-235.

Bradley, P., Horn, G., & Bateson, P. (1981). Imprinting: An electron microscopic study of chick hyperstriatum ventrale. *Experimental Brain Research, 41*, 115-120.

Bradshaw, J. L., & Bradshaw, J. A. (1988). Rotational and turning tendencies in humans: An analog of lateral biases in rats? *International Journal of Neuroscience, 39*, 229-232.

Bradshaw, J. L., & Nettleton, N. C. (1981). The nature of hemispheric specialization in man. *Behavioral and Brain Sciences, 4*, 51-63.

Bradshaw, J. L. & Nettleton, N. C. (1983). *Human cerebral asymmetry*. Englewood Cliffs, NJ: Prentice-Hall.

Brain, C. K., & Sillen, A. (1988). Evidence from the Swartkrans cave for the earliest use of fire. *Nature, 336*, 464-466.

Braitenberg, V., & Kemali, M. (1970). Exceptions to bilateral symmetry in the epithalamus of lower vertebrates. *Journal of Comparative Neurology, 38*, 137-146.

Bromage, T. G., & Boyd, A. (1984). Microscopic criteria for the determination of directionality of cutmarks on bone. *American Journal of Physical Anthropology, 65*, 359-366.

Bryden, M. P., & Steenhuis, R. F. (1987). Handedness is a matter of degree. *Behavioral and Brain Sciences, 10*, 266-267.

Byne, W., Bleier, R., & Houston, L. (1988). Variations in human corpus callosum do not predict gender: A study using MRI. *Behavioral Neuroscience, 102*, 222-227.

Byrne, R., & Whiten, A. (eds.) (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford: Clarendon Press.

Calvin, W. H. (1983). *The throwing madonna: From nervous cells to hominid brains*. New York: McGraw-Hill.

Calvin, W. H. (1987). On evolutionary expectations of symmetry in tool making. *Behavioral and Brain Sciences, 10*, 267-268.
Camp, D. M., Therrien, B. A., & Robinson, T. E. (1981). Spatial learing ability is related to an endogenous asymmetry in the nigrostriatal dopamine system in rats. *Society for Neuroscience Abstracts, 7*, 455.
Castellano, M. A., Diaz-Palarea, M. D., Rodriguez, M., & Barroso, A.J. (1987). Lateralization in male rats and dopaminergic system: Evidence of right-side population bias. *Physiology and Behavior, 40*, 607-612.
Cavalli-Sforza, L.L., Piazza, A., Menozzi, P., & Mountain, J. (1988). Reconstruction of human evolution: Bringing together genetic, archaeological and linguistic data. *Proceedings of the National Academy of Sciences, 85*, 6002-6006.
Chomsky, N. (1980). Rules and representations. *The Behavioral and Brain Sciences, 3*, 1-61.
Chui, H. C., & Damasio, A. R. (1980). Human Cerebral asymmetries evaluated by computed tomography. *Journal of Neurology, Neurosurgery, and Psychiatry, 43*, 873-878.
Cole, J. (1955). Paw preferences in cats related to hand preferences in animals and Man. *Journal of Comparative and Physiological Psychology, 48*, 137-140.
Collins, R. L. (1977). Toward an admissible genetic model for the inheritance of the degree and direction of asymmetry. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 137-150). New York: Academic Press.
Collins, R. L. (1985). On the inheritance of direction and degree of asymmetry. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 41-72). New York: Academic Press.
Corballis, M. C. (1981). Toward and evolutionary perspective on hemispheric specialization. *The Behavioral and Brain Sciences, 4*, 69-70.
Corballis, M. C., & Morgan, M. J. (1978). On the biological basis of human laterality: 1. Evidence for a maturational left-right gradient. *The Behavioral and Brain Sciences, 2*, 261-336.
Corbin, D. O. C., Williams, A. C., & White, A. C. (1987). Tardive dystonia: Which way do schizophrenics twist? *The Lancet*, January 31, 268-269.
Count, E. W. (1974). On the phylogenesis of the speech function. *Current Anthropology, 15*, 81-88.
Crosson, B. (1985). Subcortical functions in language: A working model. *Brain and Language, 25*, 257-292.
Davidson, I., & Noble, W. (1989). The archaeology of perception: Traces of depiction and language. *Current Anthropology, 30*, 125-137.
de Castro, J.M., Bromage, T. G., & Jalvo, Y. F. (1988). Buccal striations on fossil human anterior teeth: Evidence of handedness in the middle and early upper Pleistocene. *Journal of Human Evolution, 17*, 403-412.
de la Coste, M.C., Haworth, D.S., & Woodward, D.J. (1988). Prosencephalic asymmetries in *lemuridae. Brain, Behaviour and Evolution, 31*, 296-311.
Denenberg, V.H., Berrebi, A.S., & Fitch, R.H. (In Press). A factor analysis of the rat's corpus callosum. *Brain Research.*
Denenberg, V. H., & Yutzey, D. A. (1985). Hemispheric laterality, behavioral asymmetry, and the effects of early experience in rats. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 110-135). New York: Academic Press.
Dewberry, R. G., Lipsey, J. R., Sood, K., Moran, T. H., & Robinson, R. B. (1986). Lateralized response to cortical injury in the rat: Interhemispheric interaction. *Behavioral Neuroscience, 100*, 556-562.
Dewson, J.H. (1977). Preliminary evidence of hemispheric asymmetry of auditory function in monkeys. In S. Harnad, R. W. Doty, L. Goldstein, J. Jaynes & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 63-71). New York: Academic Press.
Diamond, M. C. (1984). Age, sex and environmental influences. In N. Geschwind & A. M. Galaburda (Eds.), *Cerebral dominance: The biological foundations* (pp. 134-146). Cambridge, MA: Harvard University Press.

Diamond, M. C. (1985). Rat forebrain morphology: Right-left; male-female; young-old; enriched-impoverished. In S. D. Glick (Ed.), *Cerebral lateralisation in nonhuman species* (pp. 73-88). New York: Academic Press.

Diamond, M. C., Murphy, G. M., Akiyama, K., & Johnson, R. E. (1982). Morphologic hippocampal asymmetry in male and female rats. *Experimental Neurology, 76*, 553-566.

Dingwall, W. O. (1988). The evolution of human communicative behavior. In F. J. Newmeyer (Ed.), *Linguistics: The Cambridge survey Vol. III: Language, psychological and biological aspects* (pp. 271-313). Cambridge: Cambridge University Press.

Drew, K. L., Lyon, R. A., Titeler, M., & Glick, S. D. (1986). Asymmetry in D-2 binding in female rat striata. *Brain Research, 363*, 192-195.

Ebling, J. (1985). The mythological evolution of nudity. *Journal of Human Evolution, 14*, 33-41.

Ehret, G. (1987). Left hemisphere advantage in the mouse brain for recognizing ultrasonic communication calls. *Nature, 325*, 249-251.

Engbreston, G. A., Reiner, A., & Brecha, N. (1981). Habenular asymmetry and the central connections of the parietal eye of the lizard. *Journal of Comparative Neurology, 198*, 155-165.

Fagot, J., & Vauclair, J. (1988a). Handedness and manual specialization in the baboon. *Neuropsychologia, 26*, 795-804.

Fagot, J., & Vauclair, J. (1988b). Handedness and bimanual coordination in the lowland gorilla. *Brain, Behavior and Evolution, 32*, 89-95.

Falk, D. (1978). Cerebral asymmetry in Old World monkeys. *Acta Anatomica, 101*, 334-339.

Falk, D. (1980). Language, handedness and primitive brains. Did the australopithecines sign? *American Anthropologist, 82*, 72-78.

Falk, D. (1987). Hominid paleoneurology. *Annual Review of Anthropology, 16*, 13-30.

Falk, D., Cheverud, J., Vannier, M. W., & Conroy, G. C. (1986). Advanced computer graphics technology reveals cortical asymmetry in endocasts of rhesus monkeys. *Folia Primatologica, 46*, 98-103.

Falk, D., Pyne, L., Helmkamp, R. C., & DeRousseau, C. J. (1988). Directional asymmetry in the forebrain of *Macaca mulatta*. *American Journal of Physical Anthropology, 77*, 1-6.

Fromkin, V., Krashen, S., Curtiss, S., Rigler, D., & Rigler, M. (1974). The development of language in Genie: A case of language acquisition beyond the "critical period". *Brain and Language, 1*, 81-107.

Frost, G. T. (1980). Tool behavior and the origins of laterality. *Journal of Human Evolution, 9*, 447-459.

Frumkin, L. R., & Grim, P. (1981). Is there pharmacological asymmetry in the human brain? An hypothesis for the differential hemispheric action of barbiturates. *International Journal of Neuroscience, 13*, 187-197.

Geschwind, N., & Galaburda, A. M. (1985). Cerebral lateralization: Biological mechanisms, associations and pathology. *Archives of Neurology, 42*, 428-459.

Glick, S. D., & Shapiro, R. M. (1985). Functional and neurochemical mechanisms of cerebral lateralization in rats. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 158-184). New York: Academic Press.

Goodale, M.A. (In Press). Brain asymmetries in the control of reaching. In M.A. Goodale (ed.), *Vision and action: the control of grasping*. Ablex: Norwood.

Goodman, R. A., & Whitaker, H. A. (1985). Hemispherectomy (1928-1981) with special reference to the linguistic abilities and disabilities of the residual right hemisphere. In C. T. Best (Ed.), *Hemispheric function and collaboration in the child* (pp. 121-155). New York: Academic Press.

Griffin, D. R. (1984). *Animal thinking*. Cambridge, MA.: Harvard University Press.

Güntürkün, O., & Kesch, S. (1987). Visual lateralization during feeding in pigeons. *Behavioral Neuroscience, 10*, 453-455.

Güntürkün, O., Kesch, S., & Delius, J.D. (1988). Absence of footedness in domestic pigeons. *Animal Behavior, 36*, 602-623.

Gur, R. C., Packer, I. K., Hungerbuhler, J. P., Reivich, M., Obrist, W. D., Amarnek, W. S., & Sackeim, H. A. (1980). Differences in the distribution of gray and white matter in human cerebral hemispheres. *Science, 207*, 1226-1228.

Gurusinghe, C. J., & Ehrlich, D. (1985). Sex dependent structural asymmetry of the medial habenular nucleus of the chicken brain. *Cell Tissue Research, 240*, 149-152.

Halpern, D. F. (1986). *Sex differences in cognitive abilities.* Hillside, NJ: Erlbaum.

Hamilton, C. R. (1983). Lateralization for orientation in split brain monkeys. *Behavioral Brain Research, 10*, 399-403.

Hamilton, C. R., & Vermeire, B. A. (1983). Discrimination of monkey faces by split brain monkeys. *Behavioral Brain Research, 9*, 263-275.

Hamilton, C. R., & Vermeire, B. A. (1985). Complementary hemispheric specialization in monkeys. *Society for Neuroscience Abstracts, 11*, 869.

Hamilton, C.R., & Vermeire, B.A. (1988). Complementary hemispheric specialization in monkeys. *Science, 242*, 1691-1694.

Hardy, A. (1960). Was Man more aquatic in the past? *New Scientist, 7*, 642-645.

Harré, R., & Reynolds, V. (Eds.), (1984). *The meaning of primate signals*, Cambridge: Cambridge University Press.

Heffner, H. E., & Heffner, R. S. (1984). Temporal lobe lesions and perception of species-specific vocalizations by macaques. *Science, 226*, 75-76.

Heilbronner, P.L., & Holloway, R.L. (1988). Anatomical brain asymmetries in New and Old World monkeys: Stages of temporal lobe development in primate evolution. *American Journal of Physical Anthropology, 76*, 39-48.

Heine, O., & Galaburda, A. M. (1986). Olfactory asymmetry in the rat brain. *Experimental Neurology, 91*, 392-398.

Hewes, G.W. (1973). Primate communication and the gestural origin of language. *Current Anthropology, 14*, 5-24.

Hewes, G. W. (1976). The current status of the gestural theory of language origin. *Annals of the New York Academy of Sciences, 280*, 482-504.

Hewes, G.W. (1977). Language origin theories. In D. M. Rumbaugh (ed.), *Language learning by a chimpanzee: The Lana Project* (pp. 3-53). New York: Academic Press.

Holloway, R. L. (1976). Paleoneurological evidence for language origins. *Annals of the New York Academy of Sciences, 280*, 330-348.

Holloway, R. L. (1981). Culture, symbols and human brain evolution: A synthesis. *Dialectical Anthropology, 5*, 287-303.

Holloway, R. L., & de la Coste-Lareymondie, M. C. (1982). Brain endocast asymmetry in pongids and hominids: Some preliminary findings on the paleontology of cerebral dominance. *American Journal of Physical Anthropology, 58*, 101-110.

Horn, G., & Johnson, M.H. (1989). Memory systems in the chick: Dissociations and neuronal analysis. *Neuropsychologia, 27*, 1-27.

Horster, W., & Ettlinger, G. (1985). An association between hand preference and tactile discrimination performance in the Rhesus monkey. *Neuropsychologia, 23*, 411-413.

Ifune, C.K., Vermeire, B. A., & Hamilton, C. R. (1984). Hemispheric differences in split brain monkeys viewing and responding to videotape recordings. *Behavioral and Neural Biology, 41*, 231-235.

Isaac, G. L. (1983). Aspects of human evolution. In D. S. Bendall (Ed.), *Evolution from molecules to men* (pp. 509-545). Cambridge: Cambridge University Press.

Jarman, P.J. (1972). The development of a dermal shield in impala. *Journal of Zoology (London), 166*, 349-356.

Jason, G. W., Cowey, A., & Weiskrantz, L. (1984). Hemispheric asymmetry for a visuospatial task in monkeys. *Neuropsychologia, 22*, 777-784.

Jaynes, J. (1977). *The origin of consciousness in the breakdown of the bicameral mind.* Boston: Houghton Mifflin.

Jeffries, R. P. S., & Lewis, D. N. (1978). The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. *Philosophical Transactions of the Royal Society of London B, 282*, 205-323.

Jerison, H.J. (1982). The evolution of biological intelligence. In R. Sternberg (Ed.), *Handbook of intelligence* (pp. 723-791). Cambridge: Cambridge University Press.

Jungers, W. (1988). Relative joint size and hominid locomotor adaptations. *Journal of Human Evolution, 17*, 247-270.

Kilshaw, D., & Annett, M. (1983). Right and left-hand skill 1: Effects of age, sex and hand preference showing superior skill in left-handers. *British Journal of Psychology, 74*, 253-268.

Kimura, D. (1983). Sex differences in cerebral organization for speech and praxic functions. *Canadian Journal of Psychology, 37*, 19-35.

Kimura, D. & Harshman, R. A. (1984). Sex differences in brain organization for verbal and nonverbal functions. *Progress in Brain Research, 61*, 423-444.

Kolb, B., Sutherland, R. J., Nonneman, A. J., & Whishaw, I. Q. (1982). Asymmetry in the cerebral hemispheres of the rat, mouse, rabbit and cat: The right hemisphere is larger. *Experimental Neurology, 78*, 348-359.

Kuhl, P. (1988). On handedness in primate and human infants. *Behavioral and Brain Sciences, 11*, 727-729.

LaHoste, G.J., Neveu, P.J., Morméde, P., & Le Moal, M. (1989). Hemispheric asymmetry in the effects of cerebral cortical ablations on mitogen-induced lymphoproliferation and plasma prolactin levels in female rats. *Brain Research, 483*, 123-129.

Latimer, B., & Lovejoy, C.O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology, 78*, 369-386.

Leahey, T. H., & Harris, R. J. (1985). *Human learning*. Englewood Cliffs, N. J.: Prentice Hall.

Leakey, M. D., & Hay, R. C. (1979). Pliocene footprints in the Laetolil beds at Laetoli, Northern Tanzania. *Nature, 278*, 317-323.

LeMay, M. (1976). Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. *Annals of the New York Academy of Sciences, 280*, 349-366.

LeMay, M. (1985). Asymmetries of the brains and skulls of nonhuman primates. In S. D. Glick (Ed.), *Cerebral lateralization in nonhuman species* (pp. 234-246). New York: Academic Press.

LeMay, M., & Geschwind, N. (1975). Hemispheric differences in the brain of Great Apes. *Brain, Behavior and Evolution, 11*, 48-52.

Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.

Lewin, R. (1987). Four legs bad, two legs good. *Science, 235*, 969-971.

Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review, 74*, 431-461.

Lieberman, P. (1985). On the evolution of human syntactic ability. Its pre-adaptive bases—Motor control and speech. *Journal of Human Evolution, 14*, 657-668.

Lovejoy, C. O. (1981). The origin of Man. *Science, 211*, 341-350.

Lovejoy, C.O. (1988). Evolution of human walking. *Scientific American*, November, 82-89.

Lowenstein, J., & Zihlman, A. (1988). The invisible ape. *New Scientist*, December 3 (1641), 56-59.

McCasland, J.S. (1987). Neuronal control of bird song production. *The Journal of Neuroscience, 7*, 23-39.

McGlone, J. (1980). Sex differences in human brain asymmetry: A critical survey. *The Behavioral and Brain Sciences, 3*, 215-263.

McGlone, J. (1986). The neuropsychology of sex differences in human brain organization. In G. Goldstein & R. E. Tarter (Eds.), *Advances in Clinical Neuropsychology, Vol 3* (pp. 1-30). New York: Plenum Press.

McHenry, H. M. (1982). The pattern of human evolution: Studies on bipedalism, mastication and encephalization. *Annual Review of Anthropology, 11*, 151-173.

McManus, I. C. (1976). Scrotal asymmetry in Man and ancient sculpture. *Nature, 259*, 426.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences, 10*, 247-303.

MacNeilage, P.F., Studdert-Kennedy, M.G., & Lindblom, B. (1988). Primate handedness: A foot in the door. *Behavioral and Brain Sciences, 11*, 737-744.

Malmi, W. A. (1976). Chimpanzees and language evolution. *Annals of the New York Academy of Sciences, 280*, 598-602.

Michel, G. F. (1981). Right handedness: A consequence of infant supine head-orientation preference. *Science, 212*, 685-687.

Michel, G. F. and Harkins, D. A. (1985). Concordance of handedness between teacher and student facilitates learning manual skills. *Journal of Human Evolution, 4*, 597-601.

Michel G. F. and Harkins, D. A. (1987). Ontogenetic considerations in the phylogenetic history and adaptive significance of the bias in human handedness. *Behavioral and Brain Sciences, 10*, 283-284.

Miller, G. (1981). *Language and speech*. San Francisco: Freeman.

Morgan, E. (1984). The aquatic hypothesis. *New Scientist*, April 12, 11-13.

Morgan, E. (1986). Lucy's child. *New Scientist*, December 25, 13-16.

Morris, R.D., & Hopkins, W.D. (1989). Perception of human chimeric faces by chimpanzees: Evidence for a right hemisphere asymmetry. Manuscript submitted for publication.

Morse, P. A., Molfese, D., Laughlin, N. K., Linnville, S., Wetzel, F. (1987). Categorical perception for voicing contrasts in normal and lead-treated rhesus monkeys: Electrophysiological indices. *Brain and Language, 30*, 63-80.

Nottebohm, F. (1979). Origins and mechanisms in the establishment of cerebral dominance. In M. S. Gazzaniga (Ed.), *Handbook of behavioral neurobiology, Vol 2, Neuropsychology* (pp. 295-344). New York: Plenum.

Oakley, K. P. (1981) Emergence of higher thought 3.0–0.2 Ma B.P. *Philosophical Transactions of the Royal Society of London B, 292*, 205-211.

Ojemann, G. A. (1983). Brain organization for language from the perspective of electrical stimulation mapping. *The Behavioral and Brain Sciences*, 6, 189-230.

Parker, S. T., & Gibson, K. R. (1979). A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences, 2*, 367-381.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A., Potter, D.D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkeys. Evidence from single unit and reaction time. *Behavioral Brain Research, 29*, 245-250.

Peters, M. (1988). Footedness: Asymmetries in foot performance and skill, and neuropsychological assessment of foot movement. *Psychological Bulletin, 103*, 179-192.

Petersen, M. R., Beecher, M. D., Zoloth, S. R., Green, S., Marler, P. R., Moody, D. B., & Stebbins, W. C. (1984). Neural lateralization of vocalization by Japanese macaques: Communicative significance is more important than acoustic structure. *Behavioral Neuroscience, 98*, 779-790.

Peterson, M. R., Beecher, M. D., Zoloth, S. R., Moody, D. B., & Stebbins, W. C. (1978). Neural lateralization of species-specific vocalization by Japanese macaques (*Macaca fuscata*). *Science, 202*, 324-327.

Pohl, P. (1983). Central auditory processing V: Ear advantages for acoustic stimuli in baboons. *Brain and Language, 20*, 44-53.

Pohl, P. (1984). Ear advantages for temporal resolution in baboons. *Brain and Cognition, 3*, 438-444.

Preilowski, B., Reger, M., & Engele, H. C. (1986). Handedness and cerebral asymmetry in nonhuman primates. In D. M. Taub & F. A. King (Eds.), *Current Perspectives in primate biology* (pp. 270-282). New York: Van Nostrand and Reinhold.

Premack, D. (1986). *Gavagai or the future history of the animal language controversy*. Cambridge, MA: M.I.T. Press.

Reynolds, G. P., Czudek, C., Bzowej, N., & Seeman, P. (1987). Dopamine receptor asymmetry in schizophrenia. *The Lancet*, April 25, 972.

Richards, G. (1987). *Human Evolution: An introduction for the behavioural sciences*. London: Routledge Kegan Paul.

Rogers, L. J. (1980). Lateralisation in the avian brain. *Bird Behaviour, 2*, 1-12.

Rogers, L. J. (1982). Light experience and asymmetry of brain function in chickens. *Nature, 297*, 223-225.

Rosen, G.D., Sherman, G.F., Mehler, C., Emsbo, K., & Galaburda, A.M. (1989). The effect of developmental neuropathology on neocortical asymmetry in New Zealand black mice. *International Journal of Neuroscience, 45*, 247-254.

Ruhlen, M. (1987). *A guide to the world's languages*. Stanford: Stanford University Press.

Sanford, C., Guin, K., & Ward, J. P. (1984). Posture and laterality in the bushbaby (*Galago senegalensis*). *Brain, Behavior and Evolution, 25*, 217-224.

Sherman, G. F., Galaburda, A. M., & Geschwind, N. (1982). Neuroanatomical asymmetries in nonhuman species. *Trends in the Neurosciences, 12*, 429-431.

Steklis, H. (1985). Primate communication, comparative neurology, and the origin of language re-examined. *Journal of Human Evolution, 14*, 157-173.

Stewart, M. G., Rose, S. P. R., King, T. S., Gabbott, P. L. A., & Bourne, R. (1984). Hemispheric asymmetry of synapses in chick medial hyperstriatum ventrale following passive avoidance training: A stereological investigation. *Developmental Brain Research, 12*, 261-269.

Stringer, C. B., & Andrews, P. (1988). Genetic and fossil evidence for the origin of modern humans. *Science, 239*, 1263-1268.

Susman, R.L. (1988). Hand of *Paranthropus robustus*: Fossil evidence for tool behavior. *Science, 240*, 781-784.

Susman, R.L., & Brain, T.M. (1988). New first metatarsal (SKX5017) from Swartkrans and the gait of *Paranthropus robustus. American Journal of Physical Anthropology, 77*, 7-15.

Susman, R. L., & Stern, J. T. (1982). Functional morphology of *Homo habilis. Science, 217*, 931-934.

Tan, U. (1987). Paw preference in dogs. *International Journal of Neuroscience, 32*, 825-829.

Tan, U., & Caliskan, S. (1987a). Asymmetries in the cerebral dimensions and fissures of the dog. *International Journal of Neuroscience, 32*, 943-952.

Tan, U., & Caliskan, S. (1987b). Allometry and asymmetry in the dog brain: Right hemisphere is heavier regardless of paw preference. *International Journal of Neuroscience, 35*, 189-194.

Tobias, P.V. (1987). The brain of *Homo habilis*: A new level of organization in cerebral evolution. *Journal of Human Evolution, 16*, 741-761.

Toth, N. (1985). Archaeological evidence for preferential right handedness in the lower and middle Pleistocene and its possible implications. *Journal of Human Evolution, 14*, 607-614.

Turkewitz, G. (1977). The development of lateral differences in the human infant. In S. Harnad, R.W. Doty, L. Goldstein, J. Jaynes, & G. Krauthamer (Eds.), *Lateralization in the nervous system* (pp. 251-259). New York: Academic Press.

Valladas, H., Reyss, J. L., Joron, J. L., Valladas, G., Bar-Yosef, O., & Vandermeersch, B. (1988). Thermoluminescence dating of Mousterian “Proto-Cro-Magnon” remains from Israel and the origin of modern man. *Nature, 331*, 614-616.

Vallortigara, G., Zanforlin, M., & Caillotto, M. (1988). Right-left asymmetry in position learning in male chicks. *Behavioral Brain Research, 27*, 189-191.

Vauclair, J., & Fagot, J. (1987). Spontaneous hand usage and handedness in a troop of baboons. *Cortex, 23*, 265-274.

Wada, J. A., Clarke, R., & Hamm, A. (1975). Cerebral hemispheric asymmetry in humans. *Archives of Neurology, 32*, 239-246.

Walker, S. (1987). Or in the hand or in the heart? Alternative routes to lateralization. *Behavioral and Brain Sciences, 10*, 288.

Ward, J.P. (1988). Left hand reaching preferences in prosimians. *Behavioral and Brain Sciences, 11*, 732-733.

Ward, R., & Collins, R. L. (1985). Brain size and shape in strongly and weakly lateralized rats. *Brain Research, 328*, 243-249.

Wheeler, P. E. (1984). The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution, 13*, 91-98.

Whitaker, H. A., & Ojemann, G. A. (1977). Lateralization of higher cortical functions: A critique. *Annals of the New York Academy of Sciences, 299*, 459-473.

Wind, J. (1978). Fossil evidence for primate vocalizations? In D. J. Chivers & K. A. Joysey, (Eds.), *Recent advances in primatology Vol. 3, Evolution* (pp. 87-91). New York: Academic Press.

Wind, J. (1983). Primate evolution and the emergence of speech. In E. De Grolier (Ed.), *Glossogenetics: The origins and evolution of language* (pp. 15-35). Paris: Harwood Academic Publishers.

Witelson, S.F. & Kigar, D.L. (1988). Anatomical development of the human corpus callosum: A review with reference to sex and cognition. In D.L. Molfese & S.J. Segalowitz (Eds.), *Developmental implications of brain lateralization*. New York: Guilford Press.

Witelson, S. F., & Pallie, W. (1973). Left hemisphere specialization for language in the newborn: Neuroanatomical evidence of asymmetry. *Brain, 96*, 641-646.

Wolf, M. E., & Goodale, M. A. (1987). Oral asymmetries during verbal and nonverbal movements of the mouth. *Neuropsychologia, 25*, 375-396.

Yellen, J. E. (1986). The longest human record. *Nature, 322*, 744.

Yeni-Komshian, G. H., & Benson, D. A. (1976). Anatomical study of cerebral asymmetry in the temporal lobe of humans, chimpanzees, and rhesus monkeys. *Science, 192*, 387-389.

Zappia, J. V., & Rogers, L. J. (1987). Sex differences and reversal of brain asymmetry by testosterone in chickens. *Behavioral Brain Research, 23*, 261-267.

Zimmerberg, B., Strumpf, A. J., & Glick, S. D. (1978). Cerebral asymmetry and left/right discrimination. *Brain Research, 140*, 194-196.

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HEMISPHERIC PROCESSING OF TEMPORAL INFORMATION

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ABSTRACT: The capacity of the two cerebral hemispheres for temporal processing was investigated in two experiments concerned with sensory and motor processing, respectively. The temporal processing of sensory information was examined in a task requiring simultaneity judgement of pairs of tactile stimuli delivered unimanually or bimanually. Unimanual stimulation permitted presentation of both events to the same hemisphere while bimanual stimulation involved both hemispheres and necessarily required interhemispheric communication to compare stimulus onset asynchrony (SOA). The order of presentation of asynchronous pairs determined which cerebral hemisphere was activated first. Pairs of stimuli were judged as simultaneous at longer SOAs in the bimanual than the unimanual conditions whilst unimanual left and right simultaneity thresholds did not differ. These results suggest that the two hemispheres are equally capable of temporally resolving a pair of simple tactile stimuli. A structural model proposing that temporal comparisons are carried out in the hemisphere receiving the second stimulus provides the best account of the results.

The temporal processing of motor information was examined in a task requiring the planning and execution of sequences of finger movements. A predetermined number of double-tap responses with the index and middle fingers of a given hand were required in response to a visual cue in the ipsilateral visual field. The restriction of the performance cue in each trial to the hemisphere controlling the response permitted assessment of the contribution of each cerebral hemisphere to differences in hand skill. Movement time increased linearly for both hands with increasing length of tap sequence and did not differentiate hand performance. Response preparation time, however, increased linearly with increasing task load for the preferred hand but varied quadratically for the non-preferred hand. These results indicate that differences in hand skill may be determined by the mode of response preparation within the contralateral hemisphere. They also suggest that studies of hand differences involving fixed levels of motor demand would not properly differentiate hand performance.

Together, these studies indicate that both cerebral hemispheres are capable of the temporal processing of sensory and motor information but that the hemisphere primarily involved is determined by side of stimulus or response, respectively.

Hemispheric specialisation for the processing of information has commonly been studied with techniques and tests which demonstrate sensory field advantages (see Zaidel, 1983). Many studies have con-

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centrated on hemispheric differences in the processing of verbal as opposed to visuospatial material. In this regard, the left hemisphere appears to be preferentially specialised for the processing of verbal information (see Geffen & Quinn, 1984) whilst the right hemisphere appears to play a major role in many nonverbal cognitive functions such as pattern or spatial analysis (see Milner, 1971; Bradshaw & Nettleton, 1981). Few studies have addressed the issue of hemispheric contribution to the processing of temporal as opposed to spatial information (see Mills & Rollman, 1980) though some have suggested that temporal processing takes place in the hemisphere dominant for speech since speech may be regarded as one form of this type of processing (e.g. Efron, 1963; Schwartz & Tallal, 1980). However, in assessing this matter, it would seem prudent to distinguish between the temporal processing of sensory as opposed to motor information since speech is predominantly a motor skill. This paper reports two independent experiments carried out to assess hemispheric contributions to the temporal processing of information in sensory and motor modalities, respectively. The first experiment investigated hemispheric differences in the sensory discrimination of temporal order whilst the second was concerned with the hemispheric basis of handedness in fine motor skills.

EXPERIMENT 1: THE TEMPORAL PROCESSING OF SENSORY INFORMATION

The few studies that have investigated hemispheric differences in the sensory discrimination of temporal order have tended to support the view that there is left hemisphere specialisation or superiority for this sort of judgement (Efron, 1963; Mills & Rollman, 1980). The experimental approach taken by these studies has required a judgement of whether or not pairs of bilateral stimuli are delivered simultaneously. Laterality for temporal judgement has been inferred on the basis that the stimulus onset asynchrony threshold for simultaneity judgement was smaller when the right-sided stimulus preceded the left-sided stimulus than when vice-versa. This explanation assumes that lateralised signals are initially directed to the contralateral hemisphere via contralateral sensory pathways (Corkin, 1978; Darian-Smith, 1982; Desmedt & Bourguet, 1985), that the comparison of lateralised signals requires the passage of at least one of the signals across the corpus callosum and that there is some intrahemispheric timing mechanism which ultimately compares the signals as a basis for judgement. The modelled relationship (see Mills & Rollman, 1980) between psychophysical temporal order thresholds and neural events for left hemisphere specialisation is shown in Fig-

ure 1a. The psychophysical data cited above fit both this model (Left specialisation) and one in which judgement is always performed in the hemisphere receiving the first stimulus but more efficiently in the left hemisphere (Left asymmetry).

The purpose of the present experiment was to investigate hemispheric differences in the tactile discrimination of temporal order under conditions of both bilateral and unilateral finger stimulation, since a comparison between these conditions should discriminate between the specialisation and asymmetry models described above. In the case of left specialisation, there should be no difference between unilateral left and unilateral right hand thresholds and these should themselves be intermediate to the two bilateral condition thresholds (see Figure 1). In the case of left asymmetry, unilateral right hand judgements should simply be smaller than unilateral left hand judgements. Thus, in the terms of Figure 1a, the value of T which reflects the resolution of the hypothetical, intrahemispheric timing process associated with temporal judgement would be greater for the right compared to the left hemisphere. The use of discrete tactile stimulation to the distal portion of the limbs was chosen in this experiment since it has now been shown that the transmission of sensorimotor information between these locations and the cerebral cortex is exclusively cross-lateralized (Darian-Smith, 1982).

METHOD

Subjects

Subjects were 4 male and 8 female adult volunteers between the ages of 17 and 37 years. All subjects were classified as right-handed using the six primary questions of Annett's handedness questionnaire (Annett, 1970a) and as left hemisphere language dominant according to discriminant function analysis of measures obtained during dichotic monitoring of word lists (Geffen & Caudrey, 1981). Normal hearing was assessed using pure tone audiometry with the maximum acceptable hearing loss on each ear being 25 decibels (ISD) between 250 and 8000 Hz.

Task

The task required subjects to complete series of trials in which they judged whether two point stimuli presented to separate fingers were delivered simultaneously (YES response) or not (NO response). The stimulus onset asynchrony (SOA) for each consecutive trial of a series was determined according to a variation of the PEST (parame-

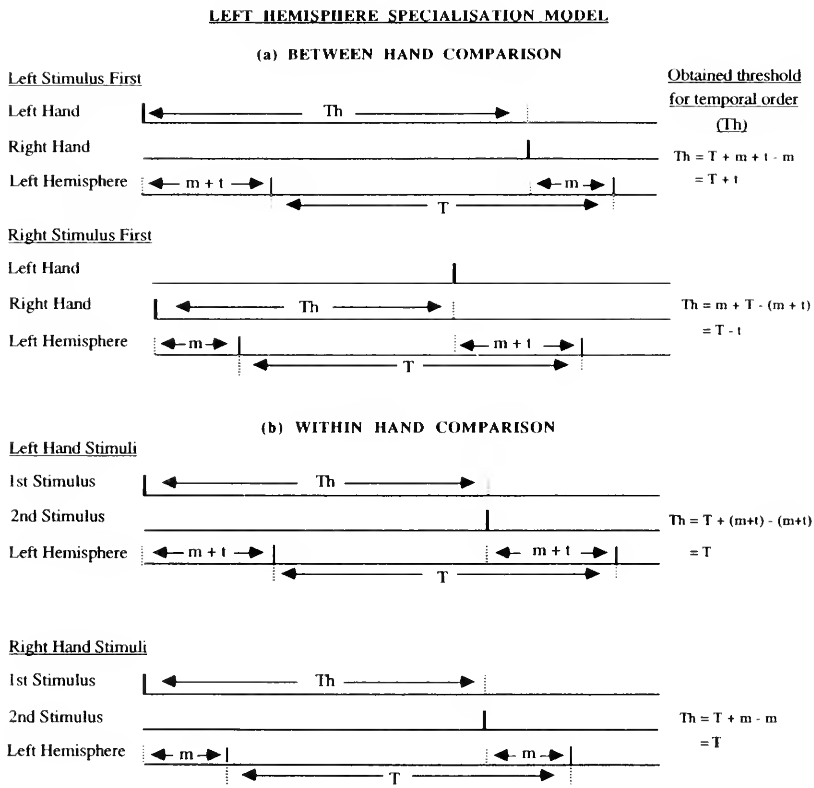

FIGURE 1. Temporal processing model based on the hypothesis of left hemisphere specialisation for the temporal resolution of consecutive pairs of tactile events. A right hand stimulus takes **m** ms to be transmitted to the left hemisphere via the exclusive contralateral pathway for digital touch information. The left hand stimulus takes **m + t** ms to reach the left hemisphere since it must additionally cross the corpus callosum (**t** ms) after contralateral transmission to the right hemisphere (**m** ms). The respective arrival of two neural events in the left hemisphere must be separated by at least **T** ms for the perceptual discrimination of the stimulus events they represent. (a) *Between-hand comparisons*: the psychophysical threshold for perceptual discrimination (**Th**) differs according to whether the left hand stimulus precedes the right hand stimulus (**T + t** ms) or the right hand stimulus precedes the left (**T − t** ms) (adapted from Mills and Rollman 1980) (b) *Within-hand comparisons*: the psychophysical threshold for perceptual discrimination (**Th = T** ms) is not affected by hand of stimulation. This model predicts that the threshold for within-hand comparisons will be intermediate to the two between-hand thresholds.

ter estimation by sequential testing) algorithmic technique (see Taylor & Creelman, 1967; Findlay, 1978) for psychophysical threshold determination. Each series of trials continued under the control of the PEST algorithm until the threshold SOA for simultaneity judgement in that series was determined or the series abandoned. The stimuli were of fixed duration (10 ms) and constant amplitude (1 mm of skin depression) and were presented mechanically with timed onset under computer control (PDP-11/34). Auditory cues from the mechanical operation were masked by binaural pink noise presented continuously through headphones during each series of trials. Pink noise levels were adjusted according to the hearing levels of the subject.

Each trial commenced with the presentation of two stimuli separated by an SOA appropriate to that trial (as determined by the PEST algorithm). A judgement was required after each trial. If no response was received within 3 s following presentation of a stimulus pair, a warning tone was presented through headphones instructing the subject to respond immediately. The tone was then repeated every 3 s until either response was received or the series abandoned.

Parameter Estimation by Sequential Testing (PEST)

This technique allows threshold parameter estimation in as few trials as possible for a given level of precision. In contrast to classical psychophysical techniques where the test values of the parameter are determined in advance, PEST uses an adaptive method in which the value adopted for any trial is determined by rules (see Findlay, 1978) which operate upon trial history. By applying PEST rules to the present task, an initial SOA is gradually reduced by steps. When the rules indicate that the threshold sought has been passed, the step direction is reversed and the SOA gradually increased by steps until a second reversal in step direction is required. Following each such reversal, the step size is reduced. The process continues until the step size falls below a predetermined value chosen to provide the required degree of precision in threshold estimation. The SOA at the termination of a series provides the series estimate of threshold.

Design

Subjects completed six test blocks of trials in each of two testing sessions no more than a week apart. In one session subjects were required to indicate their judgements verbally and in the other by bipedal depression of a two-way footswitch. The order of these sessions was counterbalanced over subjects. Verbal and non-verbal response modes were tested due to the suggestion (Efron, 1963) that verbal expression of temporal judgements may 'prime' the left hemisphere in

left dominant subjects and thereby prejudice threshold determination. It was assumed that the use of a bipedal footswitch ensured both non-verbal response and activation of both hemispheres during response. Each session commenced with practice on the task during which the smallest SOA at which a NO response could be confidently expected was estimated. This estimate was used to determine the lower limit of a 15 ms range of initial SOA values for the six test blocks. The initial SOA for these blocks was varied randomly within this range.

In each of two blocks of each session, stimulus pairs were presented to the index and middle finger of the left hand (Within Left condition), the index and middle finger of the right hand (Within Right condition) and the index fingers of both hands (Between Hands condition). The order of finger stimulation during asynchronous trials (SOA>0) was counterbalanced over the two blocks for each condition within each session. Thus, in half the sequences for each within-hands condition the index finger was stimulated first and in the other half the middle finger was stimulated first. Similarly, in half the sequences for the between-hands condition the index finger of the left hand was stimulated first and in the other half the index finger of the right hand was stimulated first. The mapping of finger to stimulator was counterbalanced over subjects within condition.

Each trial block consisted of four randomly interwoven sequences of trials with each sequence controlled independently by a governing PEST algorithm. The initial and termination step sizes for each block were 8 and 1 ms, respectively. If a sequence was not terminated by 50 trials then it was abandoned. The simultaneity threshold estimate for a block was the mean termination SOA from completed sequences within that block.

Procedure

At the beginning of each block subjects were instructed about the task and asked to rest their fingers lightly on the stimulator housings throughout each block, to avoid pressing down and to keep all fingers still since finger movement has been found to interfere with tactile perception (Angel, Weinrich & Rodnizky, 1986). They were asked to focus their attention on a midline point about 90 cm in front of them at eye level. In the session requiring verbal response, subjects were asked to respond ‘Yes’ when they judged that stimuli were simultaneous and ‘No’ when they judged that they were not. In the foot response condition, they were instructed to press forward with the toes of both feet for a ‘Yes’ response and with both heels for a ‘No’ response. There was a 5 min rest between each block of trials.

Apparatus

Two mechanical tactile stimulators were placed in a line extending forward at 90 degrees to the vertical of the body midline. They were secured in metal housings 1.5 cm in diameter and 0.75 cm apart. Each stimulator consisted of a thin rod attached at its base to a driving solenoid. When charged, the solenoid thrust the rod vertically upwards through the central core of a cylindrical metal reel. At the height of the thrust, the rod projects vertically upwards from the concave surface of the cylinder on which rests the palmar surface of the fingertip to be stimulated. Stimulus delivery was under control of a PDP-11/34 computer programmed with the PEST algorithm. Foot responses were registered on a bipedal, heel-toe rocker switch which was also connected to the computer and provided automatic feedback to the PEST algorithm for computation of the stimulus values for the following trial. Verbal responses were entered directly by the experimenter on the computer keyboard.

RESULTS AND DISCUSSION

The mean simultaneity threshold values obtained from each block were analysed by planned comparisons with repeated measures analysis of variance (SPSS-X MANOVA) on the factors of Response mode (Footswitch, Voice), Hand Condition (Between, Within-Left, Within-Right), Stimulus order (Left hand vs Right hand first for the between-hand condition; Index finger vs Middle finger first for the within-hand conditions). The mean and individual threshold scores for these factors are shown in Table 1.

The reliability of the PEST technique employed for threshold measurement was assessed by confirming that there was no significant effect of stimulus order on threshold values in either of the within-hand stimulus conditions (see Table 1). Further analysis of the scores from the within-hand conditions found no significant main effect or interactions involving response mode or hand, indicating that simultaneity judgement was not affected by either hand of stimulus or manner of reporting. Analysis of between-hand scores also revealed no main significant effects or interactions involving mode of response or stimulus order although the latter approached significance ($F(1,11) = 3.312$, $p = 0.096$). A comparison of the mean threshold scores from each of the two between-hand conditions (left hand stimulation preceding right, right hand stimulation preceding left) with the mean of those from the within-hand conditions yielded a highly significant main effect of condition ($F(1,11) = 11.914$, $p < 0.001$).

TABLE 1
Stimulus Onset Asynchrony (SOA) Scores for Simultaneity Judgement of Pairs of Tactile Stimuli.

	(i) Between Hands		*(ii) Within Left*		*(iii) Within Right*		*(iv) IHTT Estimate*
Subject	left index before right	right index before left	index before middle	middle before index	index before middle	middle before index	
1	98	76	56	61	61	53	29
2	79	75	64	62	72	63	12
3	47	39	30	39	35	34	9
4	33	34	18	18	7	12	20
5	47	34	34	34	15	21	14
6	36	17	13	20	27	35	3
7	42	48	35	35	38	32	10
8	4	14	6	3	13	16	−1
9	18	12	18	17	12	12	0
10	13	10	6	3	6	5	6
11	79	72	56	45	58	55	22
12	24	26	12	12	15	13	12
MEAN	43	38	29	29	30	29	11
SD	29	25	20	20	23	19	9

Individual and mean scores (±s.d.) from twelve right-handed, left-hemisphere dominant subjects are combined over response condition for the two possible stimulus presentation orders within each hand condition in Experiment 1. Estimates of inter-hemispheric transmission time (IHTT) shown are calculated by subtracting mean within-hand from mean between-hand thresholds.

Post hoc testing indicated that both between-hand thresholds were significantly larger than the within-hand thresholds (see Figure 2). Examination of individual scores revealed that 10 out of the 12 subjects demonstrated this relationship. This was significant by sign test (2,12; $p = 0.019$).

Support for the view that there is exclusive left hemisphere processing of temporal information required a particular pattern of results in the present study. The processing model outlined in Figure 1 predicts firstly that threshold SOA will be largest in the between-hands condition when left hand stimulation precedes the right, smallest in the between-hands condition when right hand stimulation precedes the left and intermediate in the judgement of within-hand stimulation. None of these conditions were met. The alternative view that the left hemisphere is simply more able than the right at mediating

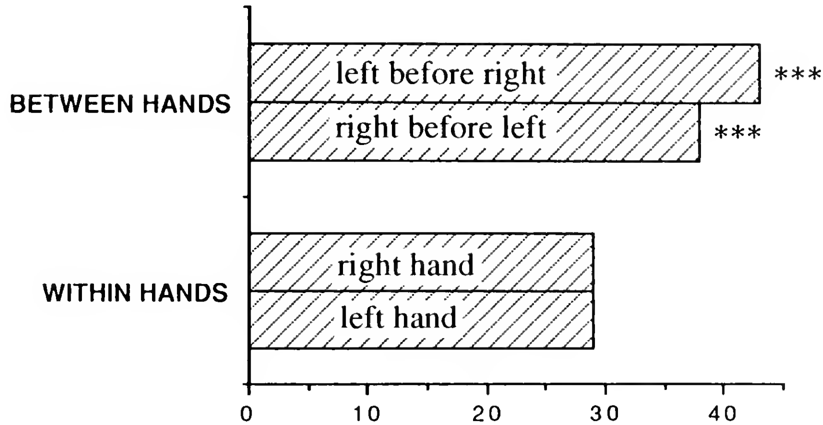

FIGURE 2. Experiment 1: Mean stimulus onset asynchrony (SOA, ms) from 12 right handed, left dominant subjects for simultaneity judgement of consecutive pairs of tactile stimuli delivered to the index fingers for between-hand judgements and to the index and middle fingers for within-hand judgements. SOA values for between-hand judgements were obtained under conditions of left-before-right hand stimulation and right-before-left hand stimulation. Within-hand judgements are the average of those obtained from index-before-middle finger and middle-before-index finger stimulation. Values have been averaged across bipedal and verbal response conditions. Individual threshold estimates were derived from four randomly interwoven PEST sequences. $^*p<0.05$.

temporal judgement was not supported either: the requirement that the within-right hand simultaneity threshold be smaller than the within-left hand threshold was not satisfied. Finally, the view (Efron, 1963) that verbal expression of temporal judgement may prejudice threshold determination in favour of the left hemisphere was not supported.

The results demonstrated that the threshold for simultaneity judgement of asynchronous tactile stimuli was higher when stimuli were presented between-hands than within-hands and that the order in which hands in the between-hands condition or fingers in the within-hand conditions were stimulated did not differ significantly. In relation to between hand stimulation, these findings are not in agreement with earlier work (Efron, 1963; Mills & Rollman, 1980) which found lower thresholds when right side stimuli preceded left side stimuli compared to the opposite order of presentation.

The failure to replicate earlier work in the tactile modality (Efron, 1963) may be due to controls employed in the present study on the effects of body hemispace on performance. It has recently been

demonstrated (see Bradshaw, Nathan, Nettleton, Pierson & Wilson, 1983) that locating the hands in right hemispace reduces reaction time to right-handed stimuli. The advantage so gained by attention to the right half of space may also apply to temporal judgements in which attention is first directed to the right, as in right before left hand stimulus judgements, compared to when it is initially directed to the left (i.e. left before right). Similar arguments may apply to those earlier studies involving auditory or visual stimulation (Efron, 1963; Mills & Rollman, 1980) which necessarily confounded stimulus condition with body hemispace. In the present study, hands were always located on the body midline during stimulation, thereby neutralising any effect of hemispace. Other factors which may be crucial to the results of the present study may include the use of a more sensitive step size (Pentland, 1980) to determine thresholds (1 ms vs 5 ms), the use of a technique with greater specificity for determining the language dominant hemisphere (Geffen & Caudrey, 1981) and the use of within-hand threshold estimates for assessing the significance of between-hand threshold values.

The results of this experiment suggest that both hemispheres have equivalent capacity for simultaneity judgements. The explanatory model shown in Figure 3 assumes as before that lateralised signals are initially directed to the contralateral hemisphere via contralateral sensory pathways, that the comparison of lateralised signals requires the passage of at least one of the signals across the corpus callosum and that there is some intra-hemispheric timing mechanism which ultimately compares the signals as a basis for judgement. The additional assumption that judgement is performed in the hemisphere receiving the second of the two bilateral stimuli permits an interpretation of the data. This account holds that lateralised stimuli are transmitted to both hemispheres as a matter of course: initially to the contralateral hemisphere then to the ipsilateral hemisphere by passage across the corpus callosum. In this way both hemispheres are prepared to compare subsequent stimuli irrespective of their side of origin with the initial stimulus. In the present experiment, 11 out of 12 subjects (92%) showed lower within-hand than between-hand thresholds as predicted by this model. Only 8 out of the 12 (67%) showed lower right-before-left than left-before-right between-hand thresholds as predicted by the left hemisphere specialisation or superiority models (see Figure 3).

Physiological data supporting the hypothesis that lateralised stimuli are transmitted to both hemispheres is available from somatosensory evoked potential (SEP) studies involving stimulation of the median nerve (Tamura, 1972; Salamy, 1978). In addition to the traditional SEPs obtained over the hemisphere contralateral to the stimulated nerve, these studies report ipsilateral responses delayed

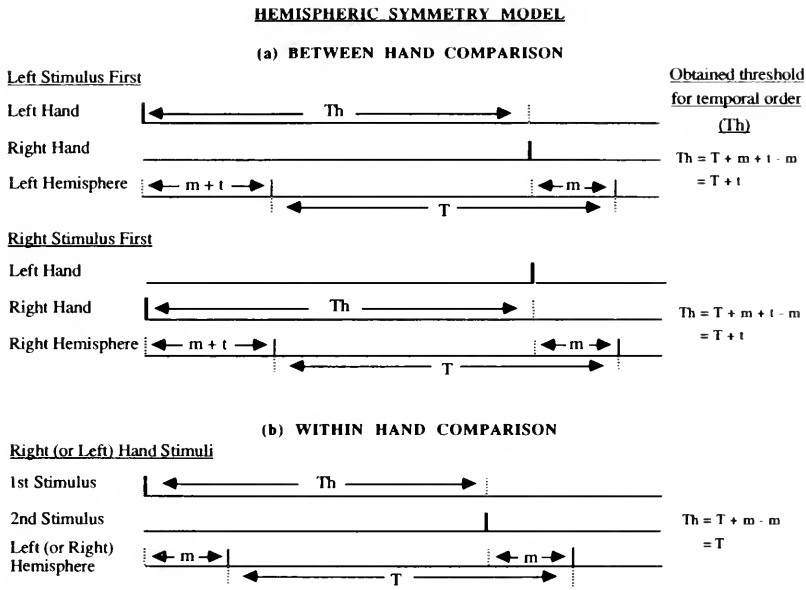

FIGURE 3. Temporal processing model based on the hypotheses that there is hemispheric equivalence for the temporal resolution of a consecutive pair of tactile events and that resolution engages the hemisphere contralateral to the second stimulus event. A stimulus takes **m** ms to be transmitted to the contralateral hemisphere and **m = t** ms to reach the ipsilateral hemisphere after crossing the corpus callosum. The arrival of neural events in the hemisphere contralateral to the second stimulus must be separated by at least **T** ms for perceptual discrimination to take place. The recognition threshold for perceptual discrimination (**Th**) is larger for (a) between-hand (**T = t** ms) than for (b) within-hand (**T** ms) stimuli.

between 4 and 8 ms compared to the contralateral wave. It was suggested that the latency difference may be due to interhemisperic transmission time via the corpus callosum though there has been a recent suggestion that interhemispheric transmission may be by volume conduction (Kakigi, 1986). Similar electrophysiological evidence has also been obtained from a visual evoked potential study involving lateralised light flashes (Rugg, Lines & Milner, 1984) which demonstrated a smaller and delayed (14 ms) N160 component over contralateral compared to ipsilateral occipital sites. As for the somatosensory studies, the delay in the ipsilateral waveform strongly suggests indirect transcallosal rather than direct transmission to the ipsilateral hemisphere.

The symmetry model of temporal judgement described in Figure

3 indicates that interhemispheric transmission time (IHTT) can be computed as the difference between the between- and within-hand simultaneity thresholds since interhemispheric transmission takes place only during between-hand stimulation. Individual estimates of IHTT ranged up to 29 ms (mean IHTT of 11 m, see Table 1). This estimate for tactile stimulation is of the same order as those from evoked potential studies such as those above, from other temporal order judgement studies (e.g. Efron, 1963) and from reaction time studies (e.g. Muram & Carmon, 1972; Moscovitch & Smith, 1979).

This experiment highlights an important distinction between corporeal hemifields (i.e. left and right hand receptor fields) and extracorporeal hemispaces (the spaces to the left and right of body midline) and the possible consequences of confounding them not only in tactile but also in visual and auditory laterality studies (see also Bradshaw, Nathan, Nettleton, Pierson & Wilson, 1983). It has been suggested above that previous experimental support for hemispheric asymmetry in temporal judgement may be an artifact of attentional biases to right hemispace. This issue can be resolved by experimental manipulation of hemispace and hemifield and a comparison of their relative effects on temporal judgement thresholds using the tactile modality.

EXPERIMENT 2: THE TEMPORAL PROCESSING OF MOTOR INFORMATION

'Handedness' or the preferential and superior use of one hand (the right in 90% of the population) to perform complex fine motor tasks has been documented historically and cross-culturally (Annett, 1985). Hand differences have a powerful genetic component (Newman, 1928; Rife, 1948), remain essentially unchanged during growth (Annett, 1970b) and persist in the face of extensive practice by the nonpreferred hand, particularly in tasks that involve temporal sequencing of movements (Annett, Annett, Hudson & Turner, 1979; Annett, Hudson & Turner, 1974; Peters, 1976, 1981). They have been shown not to be related to differences in peripheral nerve conduction (Tan, 1985). It would appear, therefore, that handedness arises from central processing differences that are permanent in nature. Further, since the distal musculature is discretely contralaterally controlled (Ghez, 1981) the asymmetry appears to be related to differences between the cerebral hemispheres. A cerebral asymmetry basis for hand differences is consistent with other left-right performance differences such as those related to language and spatial functions, and is particularly relevant to asymmetries in the perception of temporal order and the production of rapidly changing sequential information

(Bradshaw & Nettleton, 1983). More recently, it was reported that performance of a concurrent verbal task impairs sequential tapping performance of both hands but the single finger tapping of only the right hand in right handed subjects (van Strien & Bouma, 1988), suggesting that the sequential ordering of a response sequence is performed by the left hemisphere.

Consistent with the above findings, handedness is particularly evident in tasks involving the complex serial organization of muscle activity (Provins, 1967). Most studies have examined movement time (as opposed to reaction time) in a variety of continuous performance tasks including finger tapping (Peters, 1976, 1980, 1981), peg placing (Annett, 1976) and tracking (Ammons & Ammons, 1970). In general, differences in movement time increase with task complexity and are often not found in simple tasks (Provins, 1967; Steingruber, 1975). However, whilst the nonpreferred hand can be trained to move as quickly as the preferred hand, the delay between successive movements remains more variable (Peters, 1981). This implies that differences in skill between the hands are related to the preparatory phase before movement onset as well as to task complexity. This view is consistent with a recent proposal that hemispheric differences in motor planning but not motor execution underlie differences between the hands for skilled tasks (Annett, 1985). In support of this Schmidt (1975) and Annett (1985) have pointed out that many skilled movements are characterized by the rapid production of movement sequences which preclude the use of feedback cues during movement.

Previous research on motor programming (Sternberg, Monsell, Knoll & Wright, 1980) has shown that reaction time increases linearly with the number of consecutive units in the response to be made on a task (typing of letter bigrams). A modified version of the task used by Sternberg was used in the present study to examine hand differences in reaction time over a range of task difficulties. The more traditional measures (movement time, accuracy and consistency) associated with subsequent movement time were also obtained. Tachistoscopic visual cues presented to either the left or right visual field signalled the contralateral hemisphere that a response sequence was to commence. Highly trained subjects were informed in advance of the number of response units required in the sequence and the hand to be used. This design permitted a precise mapping of hand and hemisphere at different levels of response complexity since finger movements are contralaterally controlled (Ghez, 1981). The specific assumptions are that, left visual field cueing and left hand response exclusively engage the right hemisphere whilst right visual field cueing and right hand response exclusively engage the left hemisphere. It was predicted that reaction time but not movement time would differentiate left and right hand performance in our highly trained

subjects but that both measures would increase with difficulty level. Eight levels of difficulty were used in the present design.

This experiment combined techniques used in neuropsychological and skill learning paradigms, and is particularly unique in that (a) the pattern of performance was assessed over a systematically increased range of response loads, and (b) motor complexity was varied independently of perceptual uncertainty which was fully controlled and maintained constant.

METHOD

Subjects

Fourteen male university undergraduates between 18 and 30 years participated in the experiment as paid volunteers. All subjects were right handed according to a 12-item questionnaire (Annett, 1970a), had normal or corrected normal vision in both eyes, no deficits in fine motor control and no history of central or peripheral neurological damage/abnormality.

Task

Subjects completed a number of trials in which they were required to focus on a central fixation stimulus and respond to a simple visual cue presented in either the left or right visual field by tapping two keys with the index and middle fingers respectively. A midline dot at eye level was the fixation point. The visual cue was a closed square ($0.5cm^2$) presented for 140 ms at 2° to the left or right of central fixation. The stimulus preceded the cue by one second and remained on until the response was initiated (see Figure 4). The re-

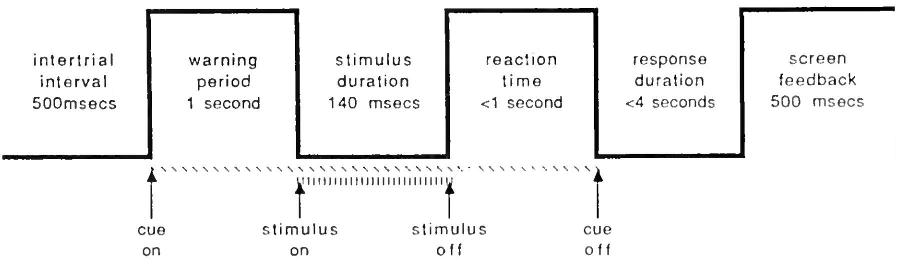

FIGURE 4. The sequence of events (from the appearance of the fixation cue to presentation of post response performance feedback) associated with a single experimental trial of the tapping task used in this experiment.

sponse consisted of a predefined number (1,2,4 or 8) of index-to-middle finger tap (response) units. Blocks of trials were given. Within each block, the response hand, visual field stimulated and number or response units was kept constant. Eye movements were monitored and trials were rejected if an eye movement occurred between the onset of the fixation cue and the first response tap.

Design

Each subject completed a required number of blocks of 20 trials in each of two experimental sessions conducted weekly at approximately the same time of day. Prior to each session subjects were advised to respond as quickly, accurately, and consistently as possible, and told that trials upon which responses were too slow, too fast, or involved eye movement would be rejected and have to be repeated. In one session, responses were made with the left hand (lh) and in the other with the right hand (rh). In half of the blocks in each session, the stimulus was presented to the left visual field (LVF), and in the other half, to the right visual field (RVF). Eight levels of response difficulty (one, two, three, four, five, six, seven, and eight response unit sequences) were completed for each visual field/hand combination within each session. Blocks were randomly ordered within sessions and the order of response hand counterbalanced over sessions. To prevent stimulus anticipation, four additional 'catch trials' occurred at random intervals within each block. In these trials no stimulus occurred following presentation of the fixation cue and the intertrial interval extended for one second. Within each session blocks were randomly ordered. The order of response hand was counterbalanced between sessions.

Procedure

Each subject completed one practice session which contained a block of ten satisfactory trials for each test condition (visual field x hand x number of response units). For a trial to be deemed satisfactory, the first tap of the trial had to occur between 150 and 1000 ms following stimulus presentation, and the correct number of taps completed in correct sequence within four seconds. A trial in any given block was rejected if response duration or latency was two standard deviations or more beyond the ongoing mean of responses so far for that block. At the beginning of each session subjects completed a warm-up block of five satisfactory trials for each experimental condition to be tested in that session. This was followed by the first block of trials. At the beginning of each block the subject was informed by screen display of the visual field in which the stimulus would occur

and the number of response units required for that block. Following each response, subjects were given visual feedback on its acceptability. Trials in a block continued until 20 satisfactory trials had been obtained.

Apparatus

Stimuli were presented on a high resolution monitor (Apple green composite) under the control of a specially programmed microcomputer (Vision AT PC compatible) which collected and timed the response sequences and related them to visual cue onset. Monitor height was adjusted so that the fixation point was at eye level on the body midline. Response sequences were mediated by a pair of microswitches attached to a response panel located on a desktop secured over the subject's lap. To minimize head movement, a velcro strap was secured across the forehead and attached to a headrest. The subject's arm and hand were restrained by weights and velcro straps respectively, so that only the distal musculature was effective. Pink noise was presented through earphones to obscure auditory cues. The microswitches were positioned on the body midline so that the index finger was located on the switch closest to the body. This was done to avoid a left-right component in the response.

Eye movements were measured electrooculographically using two cross-referenced AgACl electrodes located on the outer canthus and nasion, respectively, of one eye. The eye measured was counterbalanced with response hand.

Data Collection and Analysis

The dependent measures derived from each block of trials were: (1) reaction time: median of the time elapsed between visual cue presentation and initiation of the first tap in the response; (2) movement time: median of the time elapsed between initiation of the first and last tap in each response sequence; (3) movement consistency: the mean of the intertap intervals between successive index-middle finger taps was obtained, and the standard deviation of this mean was used to measure intraresponse unit consistency; and (4) rejections: the total number of trials rejected due to (a) incorrect number of response units, (b) incorrect finger sequencing, (c) being too fast or too slow, or (d) eye movement, and analyzed separately. Regression analyses (using GLIM) were also conducted.

Data were analysed using repeated measures factorial analyses of variance (SPSS-X MANOVA) on (a) number of Response Units (1,2,4,8), and (b) Visual Field/Hand condition (LVF/lh, RVF/rh) using polynomial trend analyses on the number of response units factor.

Data were also obtained from two crossed stimulus-response conditions (LVF/rh and RVF/lh) but will not be presented in this paper.

RESULTS AND DISCUSSION

Mean scores on all variables for the LVF/lh and RVF/rh conditions collapsed across number of response units are shown in Table 2. Reaction time, movement time, movement consistency and rejections for the two conditions as a function of number of response units are shown in Figure 5.

There was no main effect of VF/h on reaction time ($F<1$) but both linear and quadratic trend components were obtained for reaction time as a function of number of Response Units [linear $F(1,13) = 5.6$, $p<.04$; quadratic $F(1,13)=7.5$, $p<.02$]. A significant quadratic trend was found for the Response Units by VF/h interaction [$F(1,13)= 6.7$, $p<.03$]. Separate polynomial analyses over number of Response Units were then conducted for the LVF/lh and RVF/rh conditions. Reaction time in the RVF/rh condition was found to increase linearly with increasing number of Response Units [$F(1,13)=5.5$, $p<.04$], whilst reaction time in the LVF/lh condition varied quadratically [$F(1,13)=9.4$, $p<.01$—see Figure 5). Regression analyses were then conducted to generate the appropriate regression equations and determine the amount of variance accounted for by the fitted trends (Fig-

TABLE 2

Mean and Standard Deviation Scores from the Left Visual Field Stimulus/Left Hand Response (LVF/LH) and Right Visual Field Stimulus/Right Hand Response (RVF/RH) Conditions Collapsed across Number of Response Units for Reaction Time, Duration, Consistency and Number of Rejections.

	Left Visual Field/ Left Hand		*Right Visual Field/ Right Hand*	
Variables	*Mean*	*SD*	*Mean*	*SD*
Reaction time (ms)	304	91	307	75
Duration (ms)	1562	313	1509	244
Consistency (sds)	21.2	7.6	19.2	7.3
Total rejection (number)	5.7	1.1	5.8	1.2
Wrong sequence	2.6	2.8	2.9	2.9
Wrong number	1.0	1.5	0.9	1.2
Too fast/slow	0.8	0.09	0.7	0.1
Eye movements	1.4	0.6	1.3	0.5

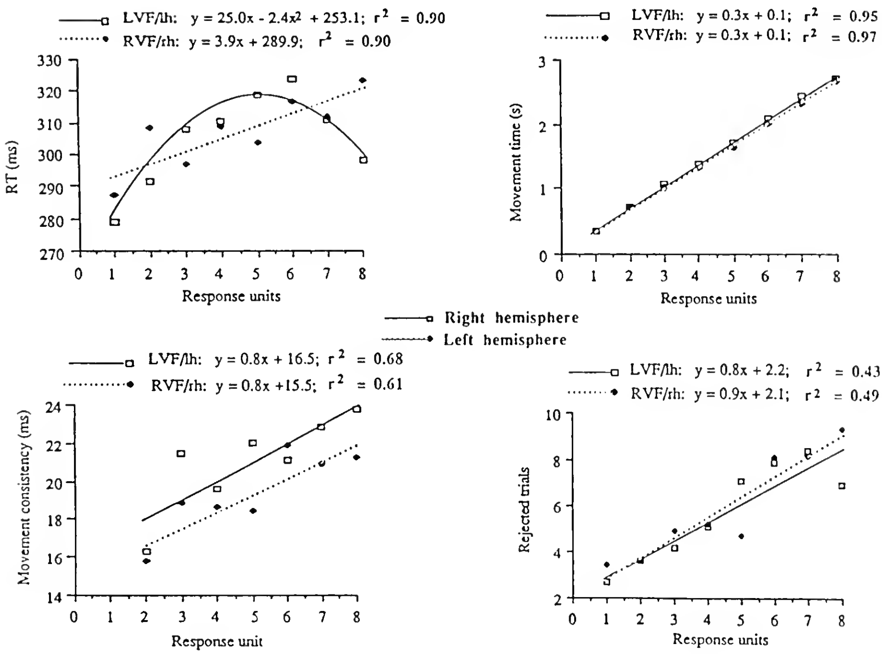

FIGURE 5. Reaction time, movement time, movement consistency and number of rejections with increasing number of Response Units for the left visual field stimulus/left hand response (LVF/LH) and right visual field stimulus/right hand response (RVF/RH) conditions (n = 14).

ure 5). In this and subsequent regression analyses, the percentage variance accounted for by the fitted trend also reflects the effect of the absolute level of each subject's performance. The linear trend in the RVF/rh condition accounted for 90.3% of the variance, and the quadratic trend in the LVF/lh condition accounted for 90.4% of the variance. Regression analyses were then conducted on the points from one to six response units to compare the linear component of LVF/lh with RVF/rh. The results indicate that preparation time in the LVF/lh condition increased over twice as steeply as the RVF/rh condition (LVF/lh:8.9; RVF/rh:4.1). The intercept with LVF/lh condition was 15 ms less than in the RVF/rh condition (274.3 vs 289.3).

There was no main effect of VF/h on either movement time, movement consistency or total number of rejections ($F<1$). Each of these measures increased linearly with number of Response Units [movement time $F(1,13)=1351.8$, $p<.001$; consistency $F(1,13)=9.9$, $p<.01$; total number of rejections $F(1,13)=28.5$, $p<.001$—see Figure 3 or 4]. There was no interaction of Response Unit and VF/h for these measures ($F<1$). Analysis of the individual error measures revealed

that the linear trend over number of Response Units resulted from trials rejected due to incorrect number of response units [$F(1,13) = 24.38$, $p < .04$] and incorrect finger sequencing [$F(1,13) = 14.8$, $p < .01$]. The number of trials rejected for being too fast, too slow or those rejected for eye movement were not effected by number of Response Units or VF/h ($F < 1$).

In summary, this experiment examined differences in fine motor skill between the left and right hand under increasing levels of performance demand. Performance involved the cued production of sequences of double taps with the index and middle fingers of one hand. The specific contribution of the left and right cerebral hemispheres to differences in hand skill was assessed by restricting performance cues to the hemisphere controlling motor preparation and movement. It was assumed that performance conditions involving left hand response to left visual field cues exclusively engaged the right cerebral hemisphere whilst right hand response to right visual field cues only engaged the left hemisphere. The pattern of results obtained indicates that the left and right hemispheres differ in the manner of preparation for the production of finely controlled motor sequences, but not in the production of the sequence itself. It suggests that the time required for motor preparation increases with increasing motor demand when the task at hand is under left hemisphere control but only to a limited extent when under right hemisphere control. Preparation time increased linearly up to six response units when the task was under right hemisphere control. Regression analyses showed that when absolute level of performance was taken into account, the fitted trends accounted for over 90% of the variance.

Whilst the effect of load on response time has been well established, very few studies have distinguished between the effect on the preparation and execution components of response. Sternberg et al. (1980) found a linear increase with load on both measures in cued verbal and bimanual typing tasks. They proposed that response to a simple cue involved not only the completion of each response unit but also the time required to organize ('unpack') each unit. Since reaction time to the cue increased linearly with the number of response units required, they concluded that unit organization prior to response must involve a serial process. The finding of a linear as opposed to a log linear relationship between preparation time and number of response units indicated that the information was not being dealt with in 'bit' form as Hick's law would predict (Hick, 1952).

Studies which have examined preparation time have generally included a stimulus choice component in the performance cue (e.g. Barnsley & Rabinovitch, 1970) which precludes an easy separation of stimulus evaluation from response organization components. The task involved in this experiment provided simple, consistent cueing

for both left and right hand performance. The critical difference obtained between left and right hand/visual field performance was reflected in the pattern of reaction times for each hand with increasing task load. The linear increase in preparation time obtained for the preferred right hand (left hemisphere control) is consistent with the serial process proposed by Sternberg et al. (1980). In this regard, the linear relationship between load and reaction time obtained by Sternberg et al. (1980) can be attributed to left hemisphere function, since both skilled typing and the rapid articulation of words may be considered to be predominantly controlled by the left hemisphere. However, the quadratic trend obtained in the present experiment for the left hand (right hemisphere control) indicates that unit organization prior to response by the nonpreferred hand may not necessarily involve serial processing. A possible explanation is that at low load levels right hemisphere preparation engages limited serial processing capacities, but takes considerably longer (over twice according to this experiment) to prepare for each additional unit than the left hemisphere, but converts to parallel processing as serial capacities are exhausted. Data supporting differential hemispheric processing strategies is provided by Oghishi (1978, cited in Bradshaw & Nettleton, 1981) who found that right but not left hand reaction times increased with the number of units of information that had to be dealt with in a choice reaction time task. No other studies examining the differential effect of response load on left versus right hand motor preparation time have been located.

GENERAL SUMMARY AND CONCLUSIONS

The data from the two experiments reported in this paper indicate that both cerebral hemispheres have the capacity for the processing of temporal information. Experiment 1 indicated that the two hemispheres have equivalent capacity for simple temporal order judgements of pairs of tactile stimuli and suggested that judgements were carried out in the hemisphere contralateral to the second stimulus. Experiment 2 examined the hemispheric processing associated with sequences of finger movements. The results of this experiment indicated that the two hemispheres differ in the manner of preparation for the production of finely controlled motor sequences, but not in the production of the sequence itself. Response preparation time by the left hemisphere of right hand (usually the preferred) movement sequences increases linearly with length of sequence, suggesting that preparation involves a serial process. Preparation time by the right hemisphere of left hand (non-preferred) movement sequences varies

quadratically with length of sequence; the particular pattern of results obtained suggests that right hemisphere response preparation converts from a limited capacity, serial process for short movement sequences to a larger capacity, order-insensitive parallel process for longer movement sequences.

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REFERENCES

Ammons, R.B., and Ammons, C.H. (1970). Decremental and related processes in skilled performance. In L.E. Smith (Ed), *Psychology of motor learning*. Chicago: Athletic Institute.

Angel, R. W., Weinrich, M. and Rodnizky, R. (1986). Recovery of somatosensory evoked potential amplitude after movement. *Annals of Neurology, 19*: 344-348.

Annett, M., (1970a). A classification of hand preference by association analysis. *British Journal of Psychology, 61*: 303-321.

Annett, M., (1970b). A growth of manual preference and speed. *British Journal of Psychology, 61*: 545-558.

Annett, M., (1976). A coordiantion of hand preference and skill replicated. *British Journal of Psychology, 67*: 587-592.

Annett, M., (1985). *Left, right, hand and brain: The right shift theory*. London: Lawrence Erlbaum Associates.

Annett, J., Annett, M., Hudson, P. T., and Turner, A. (1979). The control of movement in the preferred and nonpreferred hands. *Quarterly Journal of Experimental Psychology, 31*: 641-652.

Annett, M., Hudson, P.T., and Turner, A. (1974). The reliability of differences between the hands. *Neuropsychologia, 12*: 527-531.

Barnsley, R., and Rabinovitch, M. (1970). Handedness: Proficiency vs stated preference. *Perceptual and Motor Skills, 30*: 343-362.

Bradshaw, J.L., Nathan, G., Nettleton, N.C., Pierson, J. M., & Wilson L. E. (1983). Head and body hemispace to left and right III: Vibrotactile stimulation and sensory and motor components. *Perception, 12*: 651-661.

Bradshaw, J. L., & Nettleton, N. C. (1981). The nature of hemispheric specialization in man. *The Behavioral and Brain Sciences, 4*: 51-59.

Bradshaw, J.L., and Nettleton, N.C. (1983). *Human Cerebral Asymmetry*. NJ: Prentice-Hall.

Corkin, S. (1978). The role of different cerebral structures in somesthetic perception. In E. C. Carterette and M. P. Freidman (Eds), *Handbook of perception*, Vol VIB, (pp. 105-155). New York: Academic Press.

Darian-Smith, I. (1982). Touch in primates. *Annual Review of Psychology, 33*: 155-194.

Desmedt, J.E. & Bourguet, M. (1985). Color imaging of parietal and frontal somatosensory potential fields evoked by stimulation of medial or posterior tibial nerve in man. *Electroencephalography and Clinical Neurophysiology, 62*: 1-17.

Efron, R. (1963). The effect of handedness on the perception of simultaneity and temporal order. *Brain, 86*: 261-284.

Findlay, J.M. (1978). Estimates on probability funtions: A more virulent PEST. *Perception & Psychophysics, 23(2)*: 181-185.

Geffen, G. & Caudrey, D. (1981). Reliability and validity of the dichotic monitoring task for language laterality. *Neuropsychologia, 19*: 413-423.

Geffen, G. & Quinn, K. (1984). Hemispheric specialization and ear advantages in processing speech. *Psychological Bulletin, 96(2)*: 273-291.

Ghez, C. (1981). *Introduction to the motor system.* In E.R. Kandel and J.H. Schwartz (Eds), *Principles of neural science.* New York: Elsevier/North Holland.

Hick, W.E. (1952). On the rate of gain of information. *Quarterly Journal of Experimental Psychology, 4*: 11-26.

Kakigi, R. (1986). Ipsilateral and contralateral SEP components following median nerve stimulation: Effects of interfering stimuli applied to the contralateral hand. *Electroencephalography and Clinical Neurophysiology, 64*: 246-259.

Mills, L., & Rollman, G.B. (1980). Hemispheric asymmetry for auditory perception of temporal order. *Neuropsychologia, 18*: 41-47.

Milner, B. (1971). Interhemispheric differences in the localisation of psychological processes in man. *British Medical Bulletin, 27*: 272-277.

Moscovitch, M. & Smith, L.C. (1979). Differences in neural organisation between individuals with inverted and non-inverted writing postures. *Science, 205*: 710-713.

Muram, D. & Carmon, A. (1972). Behavioral properties of somatosensory motor interhemispheric transfer. *Journal of Experimental Psychology, 94*: 230-255.

Newman, H. (1928). Studies of human twins: II. Asymmetry reversal of mirror imaging identical twins. *Biological Bulletin, 4*: 298-315.

Pentland, A. (1980). Maximum likelihood estimation: The best PEST. *Perception & Psychophysics, 28(4)*: 377-379.

Peters, M. (1976). Prolonged practice of a simple motor task by preferred and nonpreferred hands. *Perceptual and Motor Skills, 43*: 447-450.

Peters, M. (1980). Why the preferred hand taps more quickly than the nonpreferred hand: Three experiments in handedness. *Canadian Journal of Psychology, 34*: 62-71.

Peters, M. (1981). Handedness: Effect of prolonged practice on between hand performance differences. *Neuropsychologia, 19*: 587-590.

Provins, K.A. (1967). Motor skills, handedness and behavior. *Australian Journal of Psychology, 19*: 137-150.

Rife, D. (1948). Handedness with special reference to twins. *Genetics, 25*: 178-186.

Rugg, M. D., Lines, C. R. & Milner, A. D. (1984). Visual evoked potentials to lateralized visual stimuli and the measurement of interhemispheric transmission time. *Neuropsychologia, 2*: 215-225.

Salamy, A. (1978). Commissural transmission: Maturational changes in humans. *Science, 200*: 1409-1411.

Schmidt, R. (1975). A schema theory of discrete motor skill learning. *Psychological Review, 82*: 225-260.

Schwartz, J. & Tallal, P. (1980). Rate of acoustic change may underlie hemispheric specialisation for speech perception. *Science, 207*: 1380-1381.

Steingruber, H.J. (1975). Handedness as a function of test complexity. *Perceptual and Motor Skills, 40*: 263-266.

Sternberg, S., Monsell, S., Knoll, R.L., and Wright, C.E. (1980). The latency and duration of rapid movement sequences: Comparisons of speech andtypewriting. In R.A. Cole (Ed),. *Perception and production of fluent speech*, Hillsdale, NJ: Lawrence Erlbaum Associates.

Tamura, K. (1972). Ipsilateral evoked potential responses in man. *Folia Psychiatrica et Neurologica Japonica, 26*: 83-94.

Tan, U. (1985). Velocities of motor and sensory nerve condictuin are the same for right and left arms in right- and left-handed normal subjects. *Perceptual and Motor Skills, 60*: 625-626.

Taylor, M. M. & Creelman, C. D. (1967). PEST: Efficient estimates on probability functions. *The Journal of the Acoustical Society of America, 41(4)*: 782-787.

van Strien, J.W., and Bouma, A. (1988) Cerebral organization of verbal and motor functions in left-handed and right-handed adults: Effects of concurrent verbal tasks on concurrent unimanula tapping performance. *Journal of Clinical and Experimental Neuropsychology, 10*: 139-156.

Zaidel, E. (1983). Disconnection syndrome as a model for laterality effects in the normal brain. In Hellige, J. B. (Ed), *Cerebral hemisphere asymmetry method, theory and application* (pp. 95-151), New York: Praeger.

Erratum

The title of Henretta Trent Band's article in Volume 2, Number 1 should have read: "Behavior and Taxonomy of a Chymomyzid Fly (*Chymomyza amoena*)."

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